A Phylogenetic Analysis of the Asian Catfish Families Sisoridae, Akysidae, and Amblycipitidae, with a Hypothesis on the Relationships of the Neotropical Aspredinidae (Teleostei, Ostariophysi)

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Abstract

A cladistic analysis based on 112 morphological characters was conducted for the Asiatic catfish families Sisoridae, Akysidae, and Amblycipitidae and the Neotropical family Aspredinidae. Sisoridae, Akysidae, and Amblycipitidae were divided into nearly all their currently recognized genera for the analysis, but Aspredinidae was treated as a single taxon, for a total of 20 terminal taxa. The single, fully resolved most parsimonious cladogram requires numerous modifications of the previous suprageneric classification of these fishes. The Sisoridae of previous authors was found to be a paraphyletic assemblage because a subunit of it is more closely related to the Aspredinidae than to remaining taxa so far allocated in Sisoridae. Therefore, the current Sisoridae is split into the monophyletic Sisoridae (*sensu stricto*) and Erethistidae, with Erethistidae hypothesized as the sister group to Aspredinidae. Akysidae (including *Parakysis*) is demonstrated to form a monophyletic group and to be the sister group to the clade Sisoridae (*sensu stricto*) + Erethistidae + Aspredinidae. Within Akysidae, relationships hypothesized are (*Akysis* (*Parakysis* (*Breitensteinia, Acrochordonichthys*))). Amblycipitidae is also shown to be monophyletic and is the sister group to all other families treated in the analysis. Sisoridae is composed of two major lineages, one represented by (*Bagarius* (*Sisor* (*Nangra, Gagata*))) and the other by (*Glyptothorax* (*Pseudecheneis,* "glyptosternoids")). Relationships among the genera of Erethistidae are hypothesized as (*Conta* ((*Laguvia, Pseudolaguvia*) (*Erethistoides* (*Erethistes, Hara*)))).

On the basis of the hypothesized relationships, a new classification of the whole group, named superfamily Sisoroidea, is proposed, from the level of family down to tribe and subtribe in some cases. Formal diagnoses are provided for all suprageneric clades proposed, with synonymies added for all named taxa. Evidence supporting the monophyly of some genera is also offered, along with a discussion of the possible paraphyly of some others, such as *Akysis* and *Glyptothorax*.

The evolution of two functional complexes, namely the stridulatory mechanism and the adhesive apparatus, is interpreted in light of the hypothesized relationships. Events of miniaturization and gigantism in Erethistidae and Sisoridae, respectively, are also discussed and compared with similar cases in other ostariophysans. The placement of the Neotropical Aspredinidae within an otherwise exclusively Asian clade indicates a trans-Pacific biogeographic component. The implications of this hypothesis are discussed.

Resumo

Uma análise cladística baseada em 112 caracteres morfológicos é apresentada para as famílias asiáticas Sisoridae, Akysidae, Amblycipitidae e para a família Neotropical Aspredinidae. Os

sisorídeos, akysídeos e amblycipitídeos foram subdivididos em praticamente todos os seus gêneros atualmente reconhecidos para fins de análise, enquanto que os aspredinídeos foram tratados como um único taxon, perfazendo um total de 20 terminais. O único cladograma mais parcimonioso encontrado para os dados requer várias modificações na atual classificação destes peixes. Os Sisoridae de autores prévios formam um grupo parafilético, uma vez que um de seus subgrupos está mais próximo a Aspredinidae que a outros taxa tradicionalmente alocados em Sisoridae. Em função disto, os atuais Sisoridae são divididos nas famílias monofiléticas Sisoridae (*sensu stricto*) e Erethistidae, sendo a última proposta como grupo irmão de Aspredinidae. Os Akysidae (incluindo *Parakysis*) são demonstrados formar um grupo monofilético, e formam o grupo irmão de Sisoridae (*sensu stricto*) + Erethistidae + Aspredinidae. Dentro de Akysidae, a hipótese de relações é (*Akysis* (*Parakysis* (*Breitensteinia, Acrochordonichthys*))). A família Amblycipitidae, também demonstrada monofilética, forma o grupo irmão de todas as outras famílias tratadas nesta análise. Dentro de Sisoridae, duas grandes linhagens são reconhecidas, uma representada por (*Bagarius* (*Sisor* (*Nangra, Gagata*))) e a outra por (*Glyptothorax* (*Pseudecheneis,* "glyptosternoids")). A hipótese de relações dentro de Erethistidae é (*Conta* ((*Laguvia, Pseudolaguvia*) (*Erethistoides* (*Erethistes, Hara*)))).

Com base na hipótese filogenética proposta, uma nova classificação do grupo inteiro, chamado superfamília Sisoroidea, é formulada do nível de família ao de tribo e subtribo em alguns casos. Diagnoses formais são oferecidas para todos os taxa supragenéricos, com sinonímias para todos os taxa nomeados. Sinapomorfias corroborando monofiletismo de alguns gêneros também são propostas, assim como uma discussão sobre o possível parafiletismo de alguns outros, como *Akysis* e *Glyptothorax*.

A evolução de dois complexos funcionais, a saber, mecanismo estridulatório e aparelho adesivo, é interpretada à luz da nova hipótese de relações filogenéticas. Eventos de miniaturização e gigantismo em Erethistidae e Sisoridae, respectivamente, também são discutidos e comparados com casos similares em outros Ostariophysi. A inclusão da família Neotropical Aspredinidae em um grupo que de outra forma é exclusivamente asiático indica um componente biogeográfico transpacífico. As implicações desta hipótese são discutidas.

Introduction

The families Sisoridae, Akysidae, and Amblycipitidae comprise a major portion of the catfish fauna in South and Southeast Asia. Members of these three families have been informally considered to be closely related for a long time (e.g., Day, 1871; Bridge & Haddon, 1893; Chaudhuri, 1919), and in several aspects they represent the most typical exclusively Asian siluriform assemblage. Elsewhere within the order Siluriformes, a greater degree of morphological and ecological diversification is found only in the Neotropics. Sisoridae is the largest and most diverse of the three families, containing 25 genera and approximately 120 species, with new species being discovered frequently (e.g., Kottelat, 1983; Mo & Chu, 1986; Ding et al., 1991; Zhou & Chu, 1992). Sisorids are also the most widely distributed of the three families, occurring throughout nearly the whole of South and Southeast Asia, from Iran and Turkey in the west

(Coad, 1981; Coad & Delmastro, 1985) to Sundaland, including the Indian subcontinent, Malay Peninsula, Java, Borneo, Sumatra, and part of China. Akysidae is a highly distinctive but obscure family of only four genera and about 15 species, virtually all of which are poorly known and usually are represented by few specimens in museum collections. An overview of their most speciose genus, *Akysis,* was done by He and Chen (1981). Akysids occur in the Malay Peninsula and adjacent areas, Java, Borneo, and Sumatra. The genus *Parakysis,* containing only two rather similar species from Borneo, has been traditionally included in Akysidae but was recently assigned its own family by Roberts (1989). A separate Parakysidae has been accepted by some authors (e.g., Eschmeyer, 1990; Nelson, 1994) but not others (e.g., Mo, 1991), a controversy that stems at least in part from lack of knowledge about the anatomy and phylogenetic relationships of these fishes. The Amblycipitidae, with two genera and about 10 species, occurs in

the Indian subcontinent, East Asia, Malay Peninsula and adjacent areas, Borneo, Java, and Sumatra.

Sisorids have been the object of a relatively extensive taxonomic and anatomical study. Nevertheless, the family has never been subjected to an investigation using strictly phylogenetic methodology. With the exception of one isolated effort with the genus *Pseudecheneis* (Chu, 1982), cladistics has never been applied to any level of the taxonomy of the Sisoridae. Its various genera and subfamilies, and even the family as a whole, remain recognized on the basis of informal criteria, and their monophyly has not yet been rigorously proposed or tested. The same situation holds for amblycipitids (but see a recent contribution by Chen & Lundberg, 1995) and akysids.

In view of the wide distribution of the group, a phylogenetic framework for sisorids and their relatives would be an important source of data relevant for understanding the biogeography of a large portion of Asia. Also, the great morphological variation in the group is certainly a rich ground for studies on the evolutionary significance of clade diversification. However, just as with biogeography, this area of research awaits investigation of the higher-level systematics of the Sisoridae, Akysidae, and Amblycipitidae.

A number of obstacles have hindered cladistic analyses of the Sisoridae and their closest relatives. First, many members of these groups are extremely rare in collections, and gathering representative material for anatomical studies is difficult. The internal anatomy of some genera, such as *Breitensteinia* and *Acrochordonichthys* (Akysidae), was virtually unknown prior to this study. Even for genera with several nominal species, it is sometimes impossible to obtain skeletal preparations for more than one or two individuals. Not unexpectedly, ontogenetic data are almost nonexistent for the group. Also, the absence of obvious outgroups closely related to sisorids and their relatives has prevented anatomical comparisons from being conclusive phylogenetically.

This study started as an analysis of Sisoridae; however, preliminary investigations revealed relatively weak support for sisorid monophyly and very strong support for a group composed of Sisoridae and Akysidae, plus some evidence for a more inclusive clade with Amblycipitidae. The most effective way to circumscribe and address the problem was an analysis encompassing the three families.

The scope of the analysis was further expanded by the inclusion of Aspredinidae. This Neotropical family was first explicitly proposed as closely related to Asiatic taxa (in particular Akysidae) by Ferraris (1989). Later, a number of derived similarities between aspredinids and various akysids and sisorids were recorded by de Pinna (1993). The Aspredinidae, with 10 genera and ca. 35 species widely distributed in South America, have long been a family of uncertain phylogenetic relationships. These fishes have been previously proposed as relatives of Neotropical loricarioids (Chardon, 1967, 1968), a hypothesis subsequently refuted (Baskin, 1973; Howes, 1983; Schaefer & Lauder, 1986) but not replaced by an alternative. Evidence previously reported plus additional data disclosed in a preliminary phase of this work were combined to support the working hypothesis that Amblycipitidae, Akysidae, Sisoridae, and Aspredinidae form a monophyletic ingroup. Although it was clear at that point that aspredinids were related to some level of the sisorid-akysid-amblycipitid problem, their exact position remained uncertain. One point that seemed certain, though, was that a phylogeny of the three Asian families without Aspredinidae would be incomplete and that the only consistent way to approach the problem would be to include aspredinids as a terminal taxon in the study.

Accordingly, the objectives of this work were to provide a cladistic framework for Sisoridae and its closest relatives, including aspredinids, and to propose a new higher-level classification reflecting the hypothesized relationships. This work is not intended to be a generic-level revision but instead is a first attempt at a phylogenetic understanding of Sisoridae, Amblycipitidae, Akysidae, and Aspredinidae, with a hypothesis on the monophyly of the whole group and a definition of its major subunits. The investigation focused on Sisoridae and Akysidae, which accordingly were more finely subdivided and better represented in the material examined. More in-depth studies of amblycipitids and aspredinids are currently being undertaken by X. Chen (Chen, 1994) and J. Friel (Friel, 1994), respectively.

Materials and Methods

Phylogenetic Methodology

The systematic methodology employed for proposing hypotheses of relationships was cladistic, or phylogenetic, as first proposed by Hennig (1950, 1966, 1968). Cladistics has undergone substantial

developments since Hennig's original formulation and is presently considered the standard approach for studying interrelationships among organisms. Detailed explanations of cladistic principles and foundations are currently available in a number of textbooks (e.g., Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981; Schoch, 1986; Rieppel, 1988). Recent general works focusing on more technical methodological aspects include Wiley et al. (1991) and Swofford and Olsen (1990).

Parsimony was employed to find the hypothesis best supported by the data set. Wagner (strict or simple) parsimony was used, in which character reversals and convergences are permitted and counted equally (Farris, 1983; Swofford & Maddison, 1987). Parsimony analyses were performed with the Hennig86 computer program (Farris, 1988). This program was chosen mainly because of its efficiency in calculation time. Specific information on the options and capabilities of the program were provided by Fitzhugh (1989). (See the "Phylogenetic Analysis" section for specific Hennig86 commands employed in this study.) Tree manipulations and diagnostics were done with the help of the Clados computer program (Nixon, 1992). Trees longer than the most parsimonious trees were obtained and examined with the program PAUP (Swofford, 1989), which was also used to check the most parsimonious result found with Hennig86.

Multistate characters were ordered according to similarity among character states whenever possible. Outgroup comparison provided the plesiomorphic end of the series, and other states were ordered sequentially according to their divergence from that putatively primitive condition. Therefore, more extreme expressions of a derived condition were considered evidence of monophyly for progressively less inclusive groups. This procedure is considered appropriate because similarity is the basis for any homology propositions, and the process of ordering character states is equivalent to the recognition of primary homologues.

Polarity for character states was determined by outgroup comparison. For the most part, the outgroups considered were all other catfish families available for examination. In cases where the state in outgroups varied, the algorithm of Maddison et al. (1984) was employed to decide about an optimal assignment for the plesiomorphic condition for the ingroup. The siluriform phylogeny presented by de Pinna (1993) served as a baseline for such determinations. In a few instances, ontogenetic sequences provided some information on the direction of character-state transitions. Such cases were few, though, because juvenile specimens of the taxa studied are rarely available for study.

Terminal Delimitation

It was impossible, for practical reasons, to separately analyze representatives of all known sisorid, akysid, and amblycipitid species. Therefore, some a priori decisions had to be made about the relevant terminal taxa to be considered in the analysis. Because no prior information was available on the phylogeny of sisorids and their relatives, a conservative overdivisive approach was adopted to decrease the chances of having nonmonophyletic terminals. This subdivision was also intended to decrease the number of missing entries due to terminal polymorphism, a procedure demonstrably problematic in current implementations of parsimony analysis (Nixon & Davis, 1991). The usual bottom line for subdivision was the presence of some conspicuous, obviously apomorphic trait(s) indicating that a certain assemblage of species likely composed a monophyletic group. For the most part, the sisorid genera were considered satisfactory as a starting point. Most genera in the family either are monotypic or include few species, and they are usually relatively well circumscribed by one or more putatively synapomorphic traits. The most striking exception is the genus *Glyptothorax*, with ca. 40 species (Li, 1986), which has served as a taxonomic wastebasket for species lacking the evident diagnostic characters of other genera. At present, there is little reason to believe *Glyptothorax* is monophyletic, but the taxonomic representation available for this study was not sufficient to tackle this problem. Some evidence disclosed in this work suggests that the species of *Glyptothorax* examined form a monophyletic group. Whether these characters are actual synapomorphies for the genus or only for a subgroup thereof is a question that will have to await a more complete investigation of the genus. *Laguvia* and *Pseudolaguvia,* occasionally considered as synonyms of *Glyptothorax* (e.g., Menon, 1954), were treated as separate terminals.

At the other extreme are the genera and species usually grouped together as the "glyptosternoid" sisorids (e.g., Hora & Silas, 1952a,b; Tilak, 1963, 1976; Chu, 1979; equivalent in composition to the subtribe Glyptosternina proposed in this study), which were found early in the study to form a highly corroborated monophyletic clade and were therefore treated as a single terminal.

As with Sisoridae, monophyly of Akysidae and Amblycipitidae has not previously been demonstrated or tested, and these two families were accordingly split into their presently recognized genera. Characters supporting monophyly of Aspredinidae were proposed by de Pinna (1993), and the family was therefore treated as a single terminal.

In summary, the following terminals (numbered sequentially) were considered.

Akysidae

1. *Acrochordonichthys*
2. *Akysis*
3. *Breitensteinia*
4. *Parakysis*

Amblycipitidae

5. *Amblyceps*
6. *Liobagrus*

Sisoridae

7. *Bagarius*
8. *Conta*
9. *Erethistes*
10. *Erethistoides*
11. *Gagata*
12. glyptosternoids
13. *Glyptothorax*
14. *Hara*
15. *Laguvia*
16. *Nangra*
17. *Pseudecheneis*
18. *Pseudolaguvia*
19. *Sisor*

Aspredinidae

20. Aspredinidae

(The exact composition of each of the above terminals is presented in the list of material examined.)

Autapomorphies for the terminals were actively searched for and included in the analysis. These autapomorphies should help define smaller monophyletic subunits of the family, therefore providing important background for future taxonomic and revisionary works. The inflation of the consistency index that is associated with inclusion of autapomorphies in parsimony analyses (Brooks et al., 1986; Carpenter, 1988) is not considered undesirable or "artificial" (Yeates, 1992).

Abbreviations

The following abbreviations are used for institutions and anatomical terminology.

AMNH = American Museum of Natural History, New York
ANSP = Academy of Natural Sciences of Philadelphia
BMNH = The Natural History Museum, London
CAS, CAS-SU,
CAS-IU = California Academy of Sciences, San Francisco
CMK = Collection Maurice Kottelat, formerly housed at ZSM, Munich
DUVC = Duke University Vertebrate Collection, Department of Zoology, Duke University, Durham, N.C.
FMNH = Field Museum of Natural History, Chicago
LACM = Los Angeles County Museum of Natural History
MZUSP = Museu de Zoologia da Universidade de São Paulo, São Paulo
NRM = Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Stockholm
UMMZ = Museum of Zoology, University of Michigan, Ann Arbor
USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZRC = Zoological Reference Collection, National University of Singapore
ZSM = Zoologische Staatssammlung, Munich

AC = anterior ceratohyal
ALP = anterolateral process of third hypobranchial
ANP = anterior nuchal plate
BAS = basioccipital
BB_{1-4} = basibranchials 1–4
C_{1-5} = ceratobranchials 1–5
CC = complex centrum
CF = cranial fontanel
CL = cleithrum
CO = coracoid
DC = distal condyle of first basal radial

DEN = dentary
DF$_{1-2}$ = dorsal fin spine (1, 2)
DR = distal pectoral radials
E$_{1-4}$ = epibranchials 1–4
EA = external arm of basipterygium
END = endopterygoid
F = frontal
FR = fin rays
H$_{1-3}$ = hypobranchials 1–3
HS = hemal spine
HVL = humerovertebral ligament
HY = hyomandibula
HYP = hypohyal
IA = internal arm of basipterygium
IO = infraorbital
LAC = lacrimal
LAT = lateral ethmoid
LIG = ligament
LLO = lateral-line ossicle
ME = mesethmoid
MET = metapterygoid
MNP = medial nuchal plate
N = nasal
NS = neural spine
OP = opercle
ORB = orbitosphenoid
OS = os suspensorium
PAL = palatine
PAR = parasphenoid
PC = posterior ceratohyal
PCF = paired cranial fontanel
PDR = proximal dorsal fin radial
PLR = pleural rib
PMX = premaxilla
PNP = posterior nuchal plate
POP = preopercle
PR = proximal pectoral radial
PS = pectoral spine
PTE = pterotic
QUA = quadrate
SBE = supernumerary basibranchial element
SC = sensory canal
SPH = sphenotic
SU = supracleithrum
SOC = supraoccipital
SPO = suprapreopercle
STF = supratemporal fossa
TP = tooth plate
TPR = transverse process
TRI = tripus
V = vomer
VC$_n$ = vertebral centrum n
VCB = ventral crest of basipterygium

VP$_n$ = vertebral parapophysis n
VPD = ventral process of first dorsal fin spine
WL = Weberian lamina

Material Examined

Material representative of ingroup taxa directly examined for this study is listed below. Family, genus, and species names are ordered alphabetically. The number of specimens indicated (ex) refers to those examined for this study, not necessarily the total number in the respective lot. The material was cleared and stained for bone and cartilage (BC), cleared and stained for bone only (B), radiographed (R), or dry skeleton (SK). If no designation is applied to the number of specimens, it refers to alcohol lots from which no special preparation was made. If the number of specimens (ex) exceeds that indicated for skeletal preparations (BC, R, etc.), the difference represents alcohol-preserved specimens examined. Holotypes (h), paratypes (p), and syntypes (s) are indicated immediately following the catalogue number.

Because of the highly heterogeneous sources of material, it was impossible to provide standardized locality citations. Whenever available, information on the country is provided first, followed by any additional locality data, including the major drainage system. Any additional information bearing on special conditions of certain specimens is also provided (e.g., disarticulated, uncalcified, etc.). Published accounts provided data for some outgroup and ingroup taxa not directly examined. As sources of data for outgroups, the most important papers consulted were by Arratia (1987), Ferraris (1988), Grande (1987), Lundberg (1970, 1982), Mago-Leccia (1978), Schaefer (1990), Siebert (1987), Skelton et al. (1984), Vari (1979), and Weitzman (1954, 1962). Publications on ingroup taxa provided information on species not available for direct examination and were also used to verify the consistency of some characters in species from which only one or few specimens were examined. The most important papers consulted were Chu (1982), Gauba (1962, 1966, 1967, 1968, 1969, 1970a,b), Mahajan (1966a,b, 1967a,c), Tilak (1963), and Zhou and Chu (1992). Material examined for outgroups included representatives of all nominal catfish families and some other ostariophysan groups (for a complete list of comparative outgroup material, see de Pinna, 1993).

Akysidae

Acrochordonichthys rugosus (Bleeker)—ZRC 2361a, 1 ex; Malaysia, Pahang, Taman Negara, Kuala Tahan. ZRC 4415, 1 ex, 1 BC; no data.

Acrochordonichthys ichnosoma Bleeker—MZUSP 42468, 3 ex, 1 BC; Indonesia, Kalimantan Tengah, Barito River drainage.

Akysis leucorhynchus Fowler—USNM 109636, 5 ex, 1 B, 1 BC; Thailand, north, Meping River at Chiengmai.

Akysis macronemus Bleeker—BMNH 1980.10.10: 188–192, 1 ex, 1 BC; no data.

Akysis pseudobagarius Roberts—UMMZ 155702 (p), 1 ex; Indonesia, Sumatra, Moesi River, Moeara Klingi.

Akysis sp. 1—UMMZ 214907, 10 ex, 3 BC, 1 B; Vietnam, Chau Doc, Chau Doc River, 7 km upstream from Chau Doc, CD-7, Mekong River drainage.

Akysis sp. 2—CMK 4296, 1 ex, 1 B; Kampuchea, km 117, route de Sianoukville.

Akysis sp. 3—USNM 232930, 1 ex, 1 BC (juvenile); Thailand, northeast, Nakhon Ratchasima Province, Lam Nam Mun, 1 km below dam and ca. 2 km downstream of Phimai.

Breitensteinia insignis Steindachner—AMNH 58378, 4 ex, 1 BC, 1 SK; aquarium material, no data.

Parakysis anomalopteryx Roberts—CAS 49421 (p), 2 ex, 2 BC; Indonesia, Borneo, small stream into Kapuas River, NE of Gunung Setunggul.

Parakysis verrucosa Herre—CMK 7915, 2 ex, 2 BC; Indonesia, Borneo, Kalimantan Barat, Kapuas River basin.

Amblycipitidae

Amblyceps mangois (Hamilton)—ANSP 59316, 1 ex, 1 BC; Thailand. USNM 208906, 10 ex, 1 BC. AMNH uncat., 1 ex, 1 BC (disarticulated); no data.

Liobagrus anguillicauda Nichols—AMNH 11069, 1 ex, 1 B; China, Fukian, Chungan, Hsien.

Liobagrus reini Hilgendorf—AMNH 26744, 2 ex, 1 B; Japan, Lake Biwa. USNM 089370, 4 ex, 4 B; China, Yachow Szechuan.

Sisoridae

Bagarius bagarius (Hamilton-Buchanan)—UMMZ 186793, 3 ex, 1 BC; Thailand, market at Ubol (= Ubon Ratchathani).

Bagarius yarrelli (Sykes)—AMNH uncat. 2 ex, 2 BC; aquarium material, no data. LACM 38294-55, 1 ex, SK; Pakistan, Karachi, West Wharf Fish Market; complete skeleton of large specimen, ca. 260 mm skull length.

Conta conta (Hamilton)—UMMZ 208632, 10 ex, 2 BC; Bangladesh, Sylhet, Piyain Gang River (Danki River) at Songram Punji, 1/4 mi downstream from Indian border of the Khasi and Jainta Hill region.

Erethistes pusillus Müller & Troschel—UMMZ 208697, 10 ex, 2 BC; Bangladesh, N Sylhet, Chicknagul Bazaar, 14 mi NE of Sylhet-Shillong Highway, Surma drainage.

Erethistes sp.—USNM 044759, 3 ex, 1 BC; Burma, Meetan (probable locality).

Erethistoides montana Hora—UMMZ 208745, 3 ex, 1 BC; Bangladesh, N Sylhet, Gowain River and Khal at Gowainghat, Surma drainage.

Euchiloglanis kishinouyei Kimura—USNM 120365, 3 ex, 1 BC; China, Szechuan Ts'Ao Po near Kuanshien. AMNH 15261, 1 ex, 1 BC; China.

Exostoma labiatum (McClelland)—NRM 25105, 8 ex, 1 BC; Burma, Kachin State, Kambaiti.

Exostoma sp.—USNM 130183, 3 ex, 1 BC; China.

Gagata gagata (Hamilton)—AMNH 8358, 1 ex, 1 B (disarticulated); Burma.

Gagata cenia (Hamilton)—AMNH uncat., 1 ex, 1 BC; no data.

Glyptothorax major (Boulenger)—AMNH uncat., 2 ex, 2 BC; no data.

Glyptothorax pectinopterus McClelland—BMNH 17.10.81, 2 ex, 2 BC; India, Aglar River.

Glyptothorax platypogon (Valenciennes)—USNM 087431, 6 ex, 1 BC; China, Szechuan, Suifu.

Glyptothorax sinensis (Regan)—AMNH 10265, 2 ex, 2 BC; China, Hunan, Huping, Tungting Lake.

Glyptothorax sp.—USNM 288474, 5 ex, 1 BC; Thailand, Kwai Noi River (Mekong basin), between Kanchanaburi and Sai Yok.

Glyptothorax telchitta (Hamilton)—UMMZ 208876, 1 ex; Bangladesh, Rangpur, Dharla River at Kurigram, 1/4 mi upstream from ferry ghat (dock).

Glyptothorax trilineatus Blyth—BMNH 45.1.9: 850, 1 ex, 1 BC; Nepal. UMMZ 186849, 1 ex, 1 B; Thailand, Khlong Phra Phai, 45 km NNE Chantaburi. UMMZ 208358, 1 ex; Bangladesh, Comilla, Meghna River, upstream from Chandpur, just downstream from Gumti River mouth at Kanudi. UMMZ 208458, 1 ex; Bangladesh, Dacca, Maghna River, just downstream from Gazaria, Meghna drainage.

Hara hara (Hamilton)—UMMZ 208748, 10 ex, 3 BC; Bangladesh, N Sylhet, Gowain River and Khal at Gowainghat, Surma (Meghna) drainage. FMNH 93597, 3 ex; Bangladesh, Sylhet, Gowain River Khalat Gowainghat.

Hara jerdoni (Day)—AMNH uncat. 4 ex, 4 BC; no data.

Laguvia ribeiroi Hora—UMMZ 208955, 15 ex, 5 BC; Bangladesh, Dinajpur, Maharanda River at Tetulia, near location of Dak Bungalow, Maharanda (Gangetic) drainage.

Laguvia shawi (Hora)—UMMZ 208633, 7 ex, 1 BC; Bangladesh, Sylhet, Piyain Gang River (Danki River) at Songram Punji, 1/4 mi downstream from Indian border of the Khasi and Jainta Hill region. UMMZ 208788, 1 ex; Bangladesh, Sylhet, Piyain Gang River at Songram Punji, 1.5 mi downstream from India border, Surma (Meghna) drainage.

Nangra nangra (Hamilton)—CMK 6369, 5 ex, 1 BC; India, Assam, Dibru River. FMNH 93598, 1 ex, 1 BC; Bangladesh, Comilla, Meghna River, just above Chandpurat Jahasmarcihar.

Nangra viridescens (Hamilton)—UMMZ 208725, 3 ex, 1 BC; Bangladesh, Sylhet, Sharigat Bazaar, 22 mi NE of Sylhet on Sylhet-Shillong Highway, Surma (Meghna) drainage.

Oreoglanis siamensis Smith—CMK 4351, 1 ex, 1 BC; Thailand, Doi Inthanon. USNM 118430, 3 ex, 1 BC; Thailand, Doi Angka.

Pseudecheneis sulcatus (McClelland)—FMNH 99630, 4 ex, 1 BC; Nepal, Shebu, Sabhaya Khola, Arun River. BMNH 1985.9.16:52, 1 ex, 1 BC; Nepal, Naryani River.

Pseudexostoma yunnanensis (Tchang)—NRM 25124, 5 ex, 1 BC; China, Yunnan, Irrawaddy River drainage on road to Tengchong–Burma border.

Pseudolaguvia tuberculata (Prashad & Mukerji)—UMMZ 209010, 5 ex, 1 BC; Bangladesh, Chittagong, Koilla Khal (creek), 6 mi E of Feni-Chitagong Highway on road to Ramgarh.

Sisor rhabdophorus Hamilton—BMNH 1970.6.25:2, 1 ex, 1 BC; India, Kalinadi, M. Nagar.

ASPREDINIDAE

Agmus sp.—AMNH uncat., 2 ex, 2 BC; no data. AMNH uncat., 1 ex, 1 SK; no data.

Amaralia hypsiura (Kner)—AMNH uncat., 1 ex, 1 BC; no data.

Aspredinichthys filamentosus (Cuvier & Valenciennes)—USNM 207452, 2 ex, 2 B; Brazil, off shore, 02°34′N, 49°18′W.

Aspredinichthys tibicen (Temminck)—AMNH 7094, 1 ex, 1 B; Guyana, Georgetown.

Aspredo aspredo (Linnaeus)—USNM 226072, 2 ex, 2 BC; Suriname.

Bunocephalus coracoideus (Cope)—AMNH 21815, 1 ex, 1 BC; no data.

Ernstichthys sp.—MZUSP 37814, 5 ex, 1 BC; Brazil, State of Mato Grosso, Aripuanã River, downstream from Dardanelos.

Hoplomyzon sexpapilostoma Taphorn & Marrero—AMNH uncat., 1 ex, 1 B; no data.

Xiliphius melanopterus—DUVC T-31-79, 1 ex, 1 BC; Venezuela.

Preparation Techniques and Nomenclature

Specimens were prepared for skeletal observation by the clearing and staining procedures of Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985), which allow visualization of both bone and cartilage. Several of the specimens examined were prepared prior to this study and were stained for bone only. The outline of cartilaginous structures in these specimens could usually be traced by their slightly different diffraction index in glycerol under transmitted light. In some cases, for large and/or old specimens, some modifications of the methods mentioned above had to be applied to accomplish good preparations (see de Pinna, 1993). In view of the rarity of some nominal forms, special dissecting techniques were employed to expose all relevant anatomical structures while preserving intact as many articulations as possible. In these cases, the procedure described by Weitzman (1974) was followed, with some minor alterations to fit the peculiarities of catfish anatomy.

Anatomical illustrations were prepared with the aid of a camera lucida attached to a Wild stereomicroscope. Addition and checking of details were done freehand under higher magnifications and different angles of observation. All illustrations were prepared by the author.

Nomenclatural decisions follow the rules and recommendations of the International Code on Zoological Nomenclature (ICZN, 1985). The grammar of formation of family-group names was guided by the suggestions of Steyskal (1980).

Character Description and Discussion

The characters listed below are separated according to the main region of the body where they are observed, arranged roughly in the order they are found from anterior to posterior. The account on each character begins with a sentence-like abbreviated description of the derived condition, followed by CI and RI (consistency and retention indices, respectively) values for the character under the most parsimonious hypothesis. A list of the terminal taxa with the apomorphic condition is presented in the line immediately below, following the order presented in the subsection "Terminal Delimitation." A more detailed description and discussion are presented in a separate paragraph, where the plesiomorphic condition and the justification for the hypothesized polarity are explained, along with any other pertinent observations or interpretations regarding the character.

Taxa assigned missing entries are shown within brackets, with the indication "= ?" immediately following the name (e.g., [*Sisor* = ?]). Missing entries may be assigned for a number of reasons (Nixon & Davis, 1991; Platnick et al., 1991), and each case is explained in the discussion of the respective character.

Most characters are skeletal, the only system that could be studied in the majority of the terminal taxa using the material currently available. Preliminary data indicate that a significant amount of phylogenetically informative variation also exists in myology (cf. Saxena & Chandy, 1966). However, it is presently impossible to adequately study the muscular system in many members of the ingroup, because of the unavailability of study material for many forms. With present knowledge, including these potential characters in the analysis would add such a large number of missing entries in the data matrix as to possibly obscure the phylogenetic signal from other characters. Incorporation of data from the muscular system in an analysis of the Sisoridae and their relatives will only be possible after additional material of their several rare forms becomes available.

Jaws and Related Structures

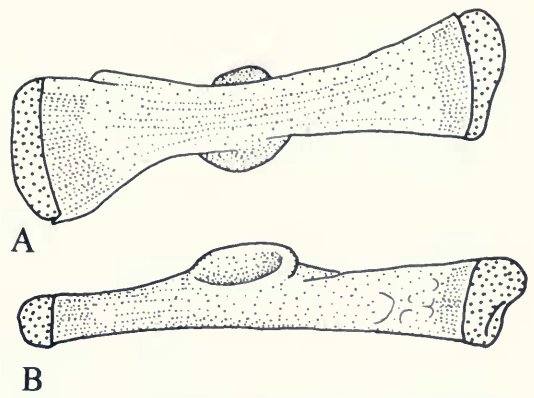1. Posterior center of ossification of palatine compressed and expanded vertically (CI = 50, RI = 0).

Fig. 1. *Dysichthys* sp., AMNH uncat., right palatine, anterior to right. **A**, lateral view. **B**, dorsal view. Larger stippling represents cartilage. Scale bar = 1 mm.

Acrochordonichthys, Akysis, Parakysis, Amblyceps, Liobagrus, Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids, *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

The plesiomorphic morphology of the posterior part of the palatine in siluriforms is that of a cylindrical ossification, roughly round in cross-section, with a short, cylindrical cartilage at the posterior tip. This is the condition seen in diplomystids, pimelodids, bagrids, and the vast majority of remaining siluriforms. In the apomorphic condition in the taxa above, the posterior portion of the palatine is laterally compressed and dorsoventrally expanded. The distal cartilage is proportionally enlarged and covers the posterior margin of the bone (Fig. 1). The expansion of the posterior portion of the palatine involves a modification in the shape of the ossification center of the bone, and not an enlargement of peripheral bone alone. This detail distinguishes the condition in the taxa above from the superficially similar state in the Amphiliidae and some Auchenoglanidinae (e.g., *Notoglanidium*), where the compressed shape is the result only of the vertical expansion of peripheral bone, with the cartilaginous center remaining cylindrical.

2. Mandibular canal entering dentary at its midsection (CI = 100, RI = 100).

Acrochordonichthys, Breitensteinia, Parakysis, [*Conta* = ?], [glyptosternoids = ?], [*Sisor* = ?], [Aspredinidae = ?].
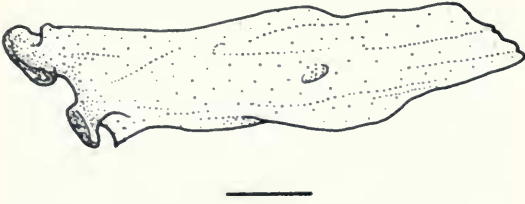
Fig. 2. *Pseudexostoma yunnanensis*, NRM 25124, right maxilla, dorsoposterior view. Scale bar = 1 mm.

The mandibular laterosensory canal in catfishes primitively enters the dentary through its ventral margin, which coincides with the anterior portion of the ventral margin of the lower jaw. In the derived condition, the canal enters the dentary at a point about the mid-depth of the posterior part of the lower jaw. The canal gradually approaches the ventral margin of the dentary as it extends anteriorly, becoming similar to the plesiomorphic condition in siluriforms along the anterior half of the lower jaw. Taxa assigned missing entries are those lacking the mandibular branch of the laterosensory canal system.

3. Mandibular laterosensory canal absent (CI = 25, RI = 0).

Conta, glyptosternoids, *Sisor*, Aspredinidae.

The mandibular portion of the laterosensory canal system, primitively present in most siluriforms and remaining ostariophysans, is apomorphically absent in the taxa above. In these taxa, the ventral branch of the preopercular laterosensory canal terminates ventrally at a pore near the posterior end of the lower jaw, not penetrating the dentary or anguloarticular. A peculiar situation is seen in aspredinids, where the dentary lacks a sensory canal but there is a branch in the soft tissue along the lower jaw. This branch often makes strong curves that do not match the profile of the dentary, indicating that its development is independent of the limits of the bone. Also, the dentary in aspredinids is a large and well-ossified bone, indicating that the canal alongside its ventral margin is not free because of bone reduction. Therefore, this canal probably represents a secondary extension of the ventral portion of the preopercular canal rather than a primitive mandibular branch. Examination of ontogenetic series of aspredinid species, not available for this study, will be the only way to test that assumption.

4. Distal tip of maxilla pointed (CI = 50, RI = 50).

Bagarius, Gagata, Nangra.

The distal end of the maxilla in siluriforms primitively has a transverse, round, or oblique edge, with a laminar morphology similar to that of the rest of the bone. In the taxa listed above, the distal portion of the maxilla is modified into a nonlamillate solid rod, with a sharp pointed tip. In some forms with the derived condition (e.g., *Bagarius, Gagata cenia, Nangra nangra*), the nonlaminar portion of the maxilla is also extremely elongate, and the longest axis of the bone is sometimes as long as the head length. The variation in length of the bone is also possibly informative about relationships but could not be adequately quantified for this analysis.

5. Maxilla dorsoventrally flat and club-shaped (CI = 100).

Glyptosternoids.

The plesiomorphic morphology of the maxilla in siluriforms is rather complex, composed of a bifurcated proximal end articulating with the anterior cartilage of the palatine and a distal portion (frequently laminar, but with shelves in three dimensions) that expands slightly at its midlength and then narrows again toward the distal tip. In all glyptosternines, the distal portion of the maxilla is markedly flat and expanded evenly toward the relatively blunt distal end (Fig. 2).

6. Interopercle narrow and elongate, its lamillate portion reduced or absent (CI = 100).

Glyptosternoids.

The interopercle in most siluriforms and other ostariophysans is a roughly triangular bone, with its posterior region much deeper than its anterior end. Other than for its anteriormost part, the bone is lamillate. In glyptosternoids, the interopercle is modified into a narrow and horizontally elongate structure, and most or all of its area is thick and nonlamillate.

7. Premaxillary dentition reduced or absent in adults (CI = 50, RI = 0).

Gagata, Sisor, [Aspredinidae = ?].

The premaxilla in catfishes primitively bears bands of numerous teeth over its ventral surface.
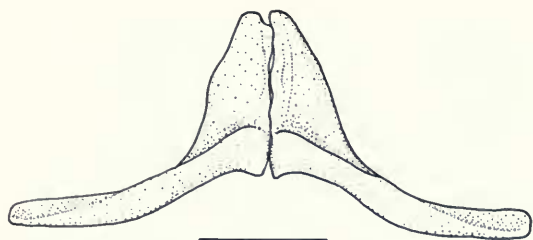
Fig. 3. *Gagata gagata*, AMNH 8358, premaxillae, anterior view. Scale bar = 1 mm.

In the derived condition, premaxillary teeth are absent in the adult stages (Fig. 3). It has been reported that young specimens of *Sisor* have at least some premaxillary teeth (Mahajan, 1966b; p. 377), which are lost later in ontogeny. Whether or not this observation applies to other taxa remains to be determined. In aspredinids, the premaxilla is edentulous in bunocephalines and toothed in aspredinines, hence the missing entry for the taxon.

8. Premaxillae with well-defined elevated facet for articulation with mesethmoid (CI = 100, RI = 100).

Gagata, Nangra, Sisor.

The dorsal surface of the premaxilla in siluriforms is primitively connected to the mesethmoid without well-defined processes or facets. In the apomorphic state, the premaxilla has a large faceted process dorsally. This structure displays a large degree of variation among the three taxa. In *Sisor,* the facet is broad and short, taking up most of the dorsal margin of the premaxilla. In *Gagata,* the facet is at the posterior surface of a large ascending process (Fig. 3) and is connected to the mesethmoid by a long cartilage. The facet is well developed in *Nangra viridescens* but is totally absent in *N. nangra,* a condition assumed to be a result of the marked reduction in the size and degree of ossification of the premaxilla in that species and not representative of the primitive condition in the genus.

A superficially similar ascending process and facet are present in the erethistid *Conta*. However, in that genus the facet is located on the anterior surface of the ascending process instead of in the posterior surface, as in all other taxa with the derived condition. The condition in *Conta* is therefore considered nonhomologous.
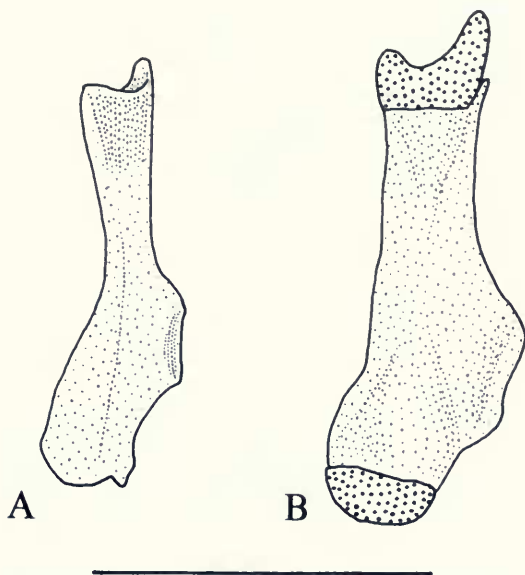

Fig. 4. Right palatines, ventromesial view. **A,** *Akysis* sp. 2, CMK 4296. **B,** *Parakysis verrucosa,* CMK 7915. Larger stippling represents cartilage. Scale bar = 1 mm.

9. Posterior half of palatine bent laterally (CI = 100, RI = 100).

[*Akysis* = ?], *Parakysis.*

In the plesiomorphic condition, the palatine in siluriforms is mostly straight from its anterior to its posterior ends as seen in dorsal view. In diplomystids, the bone can be slightly and gradually curved medially (Arratia, 1992). In the apomorphic state, the posterior portion of the palatine (posterior to its articulation with the lateral ethmoid) is abruptly bent laterally relative to the anterior portion (Fig. 4). Among the species of *Akysis* examined, the character is absent in *A. leucorhynchus* and *Akysis* sp. 1 but present in remaining representatives of the genus. This spotty distribution makes the primitive condition of the character uncertain for this taxon, which is therefore assigned a missing entry.

10. Premaxilla subdivided (CI = 50, RI = 0).

Bagarius, [glyptosternoids = ?], *Glyptothorax.*

The premaxilla in siluriforms and other teleosts is primitively composed of a single bony piece. In *Glyptothorax* and *Bagarius,* the distal portion of the premaxilla (usually directed posteriorly) is a
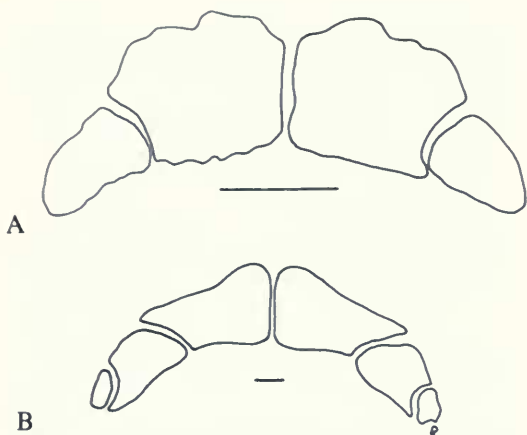
FIG. 5. Outline of premaxillae, teeth not represented. A, *Glyptothorax major*, AMNH 58410. B, *Euchiloglanis kishinouyei*, USNM 120365. Scale bars = 1 mm.

separate plate (Figs. 5, 6) connected to the remainder of the bone by connective tissue (this characteristic was first noted in *Bagarius* by Gauba [1962] and in both *Bagarius* and *Glyptothorax* by Tilak [1963]). The anterior margin of the distal piece is usually convex and fits into a corresponding concavity along the posterior margin of the proximal piece. Despite the arrangement, the two portions of the premaxilla do not seem to form a movable articulation and are firmly united to each other by rigid connective tissue. The covering of teeth is uniform and uninterrupted across the two pieces. In *Bagarius,* the two pieces overlap (but do not ankylose) in adults (Fig. 6), but in *Glyptothorax* they do not (Fig. 5A). Only one glyptosternoid examined (*Euchiloglanis kishinouyei*) shows the derived condition for this character (the species also uniquely displays further fragmentation of the lateral piece, which results in a tripartite or multipartite premaxilla; Fig. 5B). Elsewhere in glyptosternoids, a subdivided premaxilla has also been reported in *Glyptosternum reticulatum* (Gauba, 1969).

11. Presence of incisiform teeth on jaws (CI = 100, RI = 100).

Glyptosternoids, *Pseudecheneis.*

The primitive condition for jaw dentition in catfishes is to have simple conical teeth. In a few taxa there are deviations from that plesiomorphic morphology, such as in Neotropical loricarioids and most African mochokids, which may have bifur-
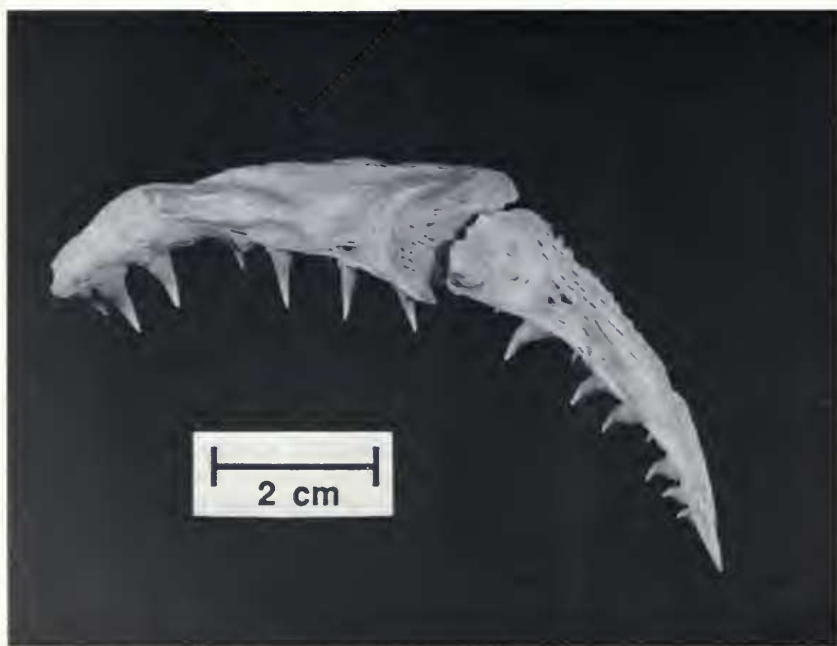

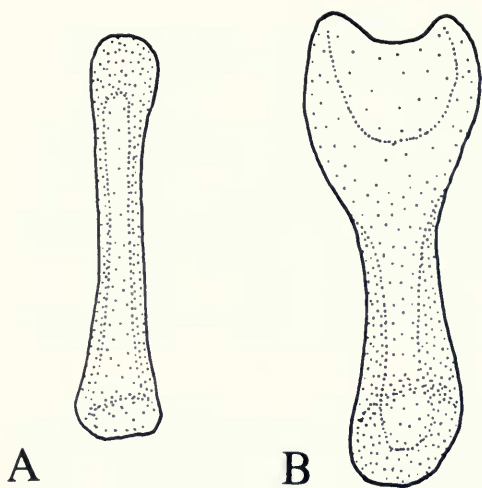FIG. 6. *Bagarius yarrelli,* LACM 38294-55, right premaxilla, dorsal view.

FIG. 7. Dentary teeth. **A,** *Pseudecheneis sulcatus,* BMNH 1985.9.16:50. **B,** *Pseudexostoma yunnanensis,* NRM 25124. Scale bar = 1 mm.

FIG. 8. *Amblyceps mangois,* ANSP 59316, metapterygoid and endopterygoid, ventromesial view. Wavy lines represent ligaments. Scale bar = 1 mm.

cated or spatulate teeth. Within the clade under study, a conspicuous derived dental morphology is seen in *Pseudecheneis* and most glyptosternoids. The jaw teeth in these taxa are strongly incisiform and usually concave in one surface (Fig. 7). Also, their distal edge is frequently straight. The teeth are conical in a few glyptosternoids, but even in these the enamel cap at the tip of each tooth is slightly larger and more prominent than in the primitive condition. These cases are postulated as partial reversals within the glyptosternoid clade. Comparative tooth morphology in some glyptosternoids was illustrated by Chu (1979, p. 75).

12. Direction of main axis of maxilla, when partly abducted, with strong ventral component (CI = 100, RI = 100).

Gagata, Nangra.

The plane of movement of the maxilla in siluriforms is mostly horizontal. As a consequence, when the bone is abducted (i.e., erect), its main axis points either laterally or laterally and slightly ventrally. In the two genera above, the maxilla is attached to the palatine in such a way that when it is abducted to a nearly 90° angle with the palatine, its main axis points strongly ventrally. The situation is most marked in *Gagata cenia,* where
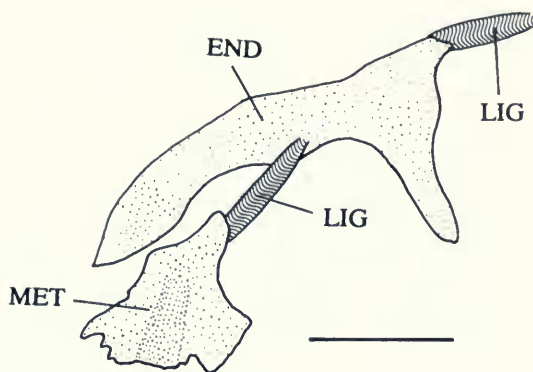
the maxilla points almost directly ventrally when partly abducted.

Suspensorium and Opercular Apparatus

13. Metapterygoid with long anterior process (CI = 50, RI = 50).

Acrochordonichthys, Akysis, Breitensteinia.

The metapterygoid in siluriforms other than diplomystids is primitively an irregular, roughly round plate of bone. Although it may have well-marked angles along its borders, it usually lacks large processes. In the taxa above, the metapterygoid has an elongate process at its anterior corner. This process, when long enough, runs alongside the ventrolateral border of the posterior part of the palatine and parallels the ventral margin of the ectopterygoid. The process is very small but is still quite evident in *Akysis macronemus.*

14. Metapterygoid with well-defined thickening for ligamentous connection with endopterygoid (CI = 100, RI = 100).

Amblyceps, Liobagrus.

The metapterygoid and endopterygoid in catfishes, when both elements are present, are connected by a sheet-like but usually poorly differentiated ligament. In amblycipitids, the ligament is narrow and very well defined, and its attachment site on the metapterygoid is delimited by an os-
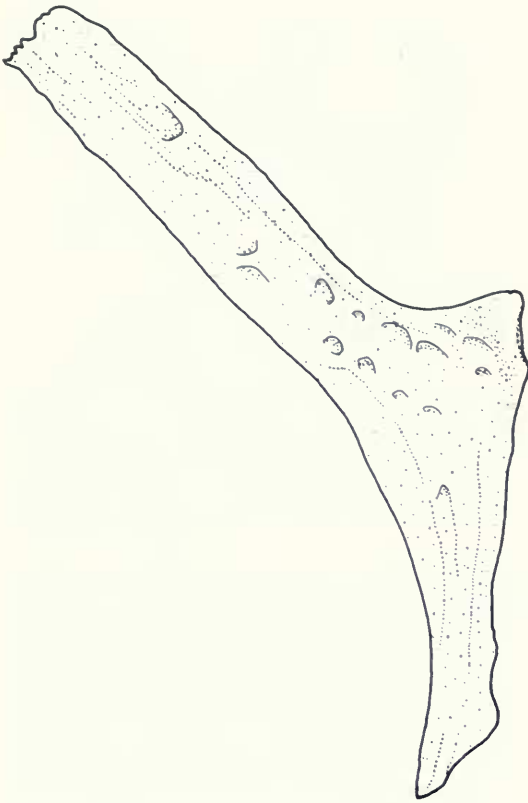
FIG. 9. *Laguvia ribeiroi*, UMMZ 208955, right opercle, lateral view. Scale bar = 1 mm.

seous thickening that forms a small globular process on the mesial margin of the bone (Fig. 8).

15. Quadrate with anterior spur-like process (CI = 50, RI = 0).

Parakysis, Amblyceps.

The anterior portion of the quadrate in catfishes primitively has no expansions extending anteriorly significantly beyond the vertical through its articulation with the lower jaw. In the taxa above, there is a large laminar extension of bone extending anteriorly from the dorsal margin of the anterior portion of the quadrate. This elongate laminar expansion extends alongside most of the lateral margin of the metapterygoid, and a conspicuous ligament connects it either with the lateral ethmoid or with the posterior region of the premaxilla (the exact point of attachment is impossible to determine from the material available).

16. Endopterygoid surrounding metapterygoid dorsally (CI = 100).

Pseudecheneis.

The meta- and endopterygoid in siluriforms primitively do not encircle one another. In *Pseudecheneis,* the endopterygoid is strongly curved (ventrally concave) to closely surround the dorsal margin of the metapterygoid.

17. Metapterygoid reduced to its center of ossification (CI = 100).

Parakysis.

The metapterygoid of siluriforms is primitively composed of a small ossification center adjacent to its articulation with the quadrate, plus a more or less extensive area of laminar bone. The laminar region usually forms the majority of the area of the metapterygoid. In *Parakysis,* the laminar portion is extremely reduced, and the metapterygoid is effectively represented only by its small, cone-shaped ossification center.

18. Very large subpreopercle (CI = 100).

Parakysis.

The subpreopercle of siluriforms is typically a tubule of bone lining the branch of the laterosensory canal between the preopercle dorsally and the lower jaw ventrally. It is commonly found in catfishes as a poorly ossified and thin-walled structure. In *Parakysis,* the subpreopercle is apomorphically modified into a large and thick-walled bone, still canal-like in morphology but far more heavily ossified than is usual in other siluriforms.

19. Opercle very narrow (CI = 100, RI = 100).

Laguvia, Pseudolaguvia, [Aspredinidae = ?].

The overall morphology of the opercle in siluriforms is that of a broad, roughly triangular bony lamina. Although there is wide variation in the shape of the bone, it is almost invariably a relatively wide plate as in other ostariophysans and teleosts in general. In the derived state, most of the laminar portion of the opercle is absent, and its remaining part is represented mostly by the regions corresponding to the dorsal and anteroventral margins of the bone in the primitive condition. The opercle thus has the form of a long thin arc with the concave portion located ventroposteriorly (Fig. 9). This apomorphic morphology

is the result of a reduction of the ossification of the central lamina of the opercle. This reduction, and the fact that some of the taxa showing this opercle modification (*Laguvia*) have a small body size, indicate that it may be a paedomorphic trait. However, another paedomorphic sisorid, *Hara jerdoni,* has a plesiomorphic condition for the opercle. The opercle in most aspredinids corresponds to the derived condition; however, at least one (*Xyliphius*) has a large opercular lamina, casting doubt on the exact coding for this character in that taxon.

20. Hyomandibula with convex anterior expansion (CI = 100, RI = 100).

Amblyceps, Liobagrus.

The posterior margin of the hyomandibula in catfishes primitively forms a simple arc not extending significantly posterior to the articular condyle for the opercle. In both genera of Amblycipitidae, the hyomandibula has a conspicuous laminar expansion posteriorly, immediately ventral to its articulation with the neurocranium. This expansion has a roughly round profile and extends posteriorly considerably beyond the articulation with the opercle.

21. Endopterygoid with spur-like process anterolaterally (CI = 100).

Bagarius.

The catfish ectopterygoid, when present, is quite irregular in shape and may have a number of angles around its margin, some of which can assume the aspect of poorly defined processes. The large ectopterygoid in *Bagarius* uniquely has a well-defined pointed process anterolaterally. This spur-like nonlaminar process extends dorsally along part of the posterior segment of the premaxilla and is ligamentously attached to it.

22. Endopterygoid bifurcated anteriorly (CI = 100, RI = 100).

Laguvia, Pseudolaguvia.

The anterior end of the endopterygoid in *Laguvia* and *Pseudolaguvia* is divided into two broad laminar arms with pointed tips. This condition contrasts with the plesiomorphic morphology of the bone seen in other catfishes (cf. character 21).

23. Condyle for opercle on hyomandibula directed ventrally (CI = 100).

Aspredinidae.

The opercular condyle of the hyomandibula is primitively directed posteriorly or slightly ventroposteriorly in siluriforms. The derived condition shows the condyle directed strongly ventrally. A similar situation is also present in most members of Clariidae. However, the number of nodes separating aspredinids and clariids in catfish phylogeny and the fact that the primitive clariid *Horaglanis* shows the plesiomorphic condition for this character (de Pinna, 1993) indicate that the two occurrences of the derived state are convergent.

Neurocranium

24. Supratemporal fossa present (CI = 33, RI = 60).

Acrochordonichthys, Akysis, Breitensteinia, Parakysis, Bagarius, Conta, Erethistes, Erethistoides, Gagata, Glyptothorax, Hara, Laguvia, Nangra, Sisor, Aspredinidae.

These taxa share a well-defined depression, usually round or triangular in shape, between the supraoccipital, pterotic, and supracleithrum bones (Fig. 10). The depression is often filled with what appears to be adipose tissue and does not serve as a site for muscle insertion. Mahajan (1966b, p. 367) referred to this structure as a "temporal groove" when noting its presence in *Sisor rabdophorus*. The degree of development of the fossa varies widely among the examined taxa that have it, reaching its largest size in the akysid *Acrochordonichthys rugosus*. It tends to be less well marked in species with heavy skull ossification and ornamentation, such as *Erethistes, Glyptothorax,* and similar forms. In these cases the fossa can be partly attenuated by additional ossification but is usually still evident from an angled dorsolateral view. The fossa is reduced in adult specimens of *Parakysis* examined but is still present as a small space adjacent to the anterior margin of the supracleithrum. It is more evident in smaller specimens of *Parakysis anomalopteryx*. The fossa is occasionally absent in some specimens of *Laguvia shawi,* but it is definitely present, albeit extremely small, in *L. ribeiroi*. The structure is also absent in the largest *Bagarius* examined (a representative of *B. yarrelli*), presumably as a result of additional os-
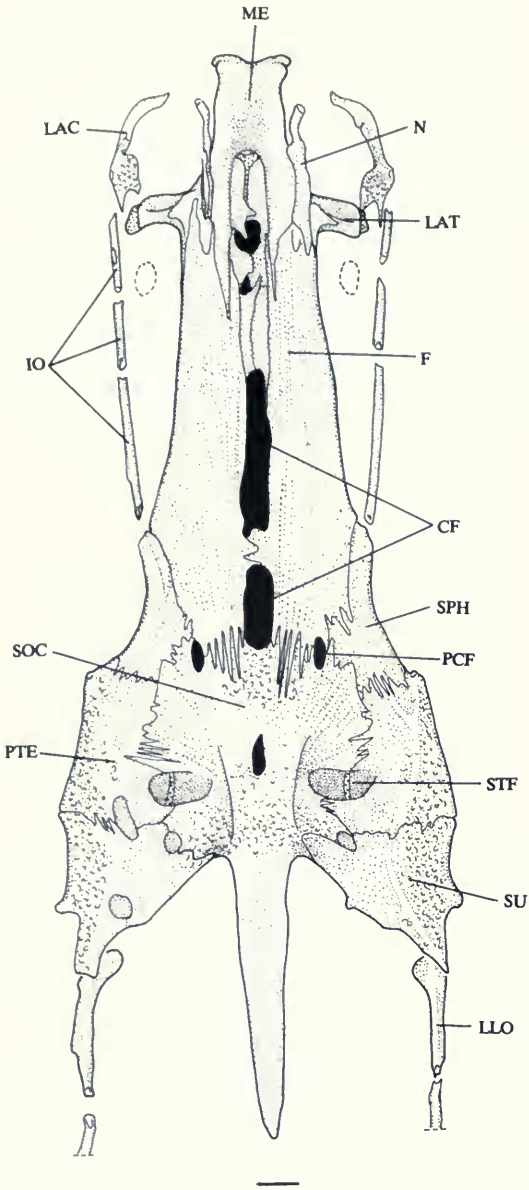
FIG. 10. *Breitensteinia insignis*, AMNH 58378, neurocranium and associated structures, dorsal view. Dotted lines outline eyes. Scale bar = 1 mm.

sification that develops in large individuals. Smaller specimens of the species have the fossa. The structure is clearly visible in aspredinids, except in *Xyliphius*, where it is largely obscured by heavy bony growth.

25. Paired fontanels among supraoccipital, frontals, and sphenotics (CI = 50, RI = 75).

Acrochordonichthys, Breitensteinia, Gagata, Nangra, Sisor.

Siluriforms primitively have two median fontanels in the neurocranium, similar to those in other otophysans. The two fontanels are usually separated by a bony strut called the epiphyseal bar. In the taxa above, the neurocranium possesses an additional paired fontanel, positioned between the frontal and supraoccipital (Fig. 10), sometimes also occupying a small area of the sphenotic. The paired fontanels are usually located at about the same transverse level as the posterior median fontanel and do not seem to serve as passage for nerves or blood vessels. They are actual fontanels, opening to the interior of the braincase, and not just depressions in bone, such as with the supratemporal fossa. The paired fontanels reach their greatest development in *Nangra nangra,* as a result of which the skull nearly lacks a roof. In *Nangra viridescens,* the paired fontanel is small and strongly displaced posteriorly, and its margins are sometimes partly coalescent with the supratemporal fossa. The paired fontanels are smallest in *Breitensteinia* and *Acrochordonichthys.*

The actual distribution of the paired fontanels may be far broader than recorded here, and it may be obliterated by additional ossification in adults of many taxa. Although absent in male aspredinids examined, for example, small fontanels are present in juvenile specimens of *Aspredo aspredo* (USNM 226072). This condition may occur in several other terminal taxa whose juveniles are currently unknown but that have heavily ossified skulls as adults. Until more information on juveniles of several other taxa becomes available, this character is defined as the presence of paired fontanels in the adult stage only. The presence of these fontanels in any stage of development may represent a character for a considerably larger clade.

26. Supracleithrum strongly attached to skull (CI = 100, RI = 100).

Acrochordonichthys, Akysis, Breitensteinia, Parakysis, Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids, *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

The complex structure forming the upper portion of the shoulder girdle in catfishes (formed by

the supracleithrum, posttemporal, and arguably the extrascapular and ossified Baudelot's ligament; see Lundberg [1975] and Fink & Fink [1981] for a discussion on this issue; for convenience, the whole structure is herein referred to as the supracleithrum) is primitively loosely connected with the posterolateral portion of the skull roof. The articulation of the supracleithrum with the skull is movable to a certain extent, and although the bony surfaces are closely set, the link is by soft connective tissue only. In the derived condition, the supracleithrum is firmly attached or ankylosed to the neurocranium, and the two elements are immovably connected either by strong connective tissue (aspredinids) or direct bone contact (all other terminal taxa above).

27. Posterior portion of supracleithrum ankylosed to margin of Weberian lamina (CI = 66, RI = 91).
    State 1: *Bagarius, Conta, Gagata, Glyptothorax, Nangra, Sisor,* Aspredinidae.
    State 2: *Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia.*

The supracleithrum in catfishes has a complex three-dimensional structure that may play a variety of structural roles in the region of the back of the skull, Weberian complex, and shoulder girdle. It is difficult to make a generalization about the primitive condition of the supracleithrum as a whole for siluriforms because it includes a number of possibly independent characters that can only be appropriately described and understood separately. In the case in question, the taxa enumerated above share a derived condition unique among siluriforms, in which the supracleithrum has a large posterior process originating about the same horizontal level as the lateral margin of the Weberian lamina. This process joins the margin of the Weberian lamina and ankyloses with it, forming a firm bony strut between the back of the skull (to which the supracleithrum is also firmly attached or ankylosed in the above taxa) and the Weberian complex (Fig. 11). Among the taxa examined, only *Glyptothorax pectinopterus* has a doubtful condition for this character because its posterior supracleithral process is poorly developed, a condition assumed to be a result of the small size of the specimens examined for that species.

This character is subdivided into two ordered states. In state 1, the posterior supracleithral pro-

cess extends to midway along the lateral margin of the Weberian lamina (Fig. 11A). In state 2, more extreme, the process extends for at least two thirds of the total lateral margin of the lamina (Fig. 11B).

28. Pterotic with shelf-like expansion laterally (CI = 100).

Aspredinidae.

The lateral margin of the pterotic in catfishes is primitively devoid of conspicuous expansions beyond the general profile of the neurocranium in dorsal view. In aspredinids, the pterotic has a large shelf-like expansion of laminar bone extending laterally well beyond the remainder of the profile of the skull. At its site of attachment, this shelf is about half the width of the skull.

29. Epioccipital with slender posterior process (CI = 50, RI = 50).

Bagarius, Gagata, Nangra.

The plesiomorphic condition of the epioccipital in siluriforms is a simple convex posterior surface without conspicuous expansions or processes. In these three taxa, the epioccipital has a well-defined, slender posterior process that is somewhat rounded or flattened in cross-section and oriented perpendicular to the main surface of the bone (Fig. 12). The process is pointed at its distal tip and seems to serve as an attachment for a ligament whose other end of attachment could not be precisely located in the material available. It attains its largest development in *Bagarius,* where it apparently becomes more heavily ossified with growth. The process is smallest but still clearly present in *Gagata cenia.* In some specimens of *Glyptothorax,* there is a slight prominence at the posterior surface of the epioccipital that may represent an incipient stage of the process. If this observation is confirmed in more detailed morphological studies, then the level of this character will have to be modified and perhaps be divided in two ordered derived states, state 1 applying to *Glyptothorax* and state 2 assigned to the assemblage above. In the meantime, *Glyptothorax* is coded as having the primitive condition.

A few other catfishes also have an epioccipital process, namely Neotropical doradoids (Chardon, 1968; Ferraris, 1988). In these taxa, however, the structure is much larger, laminar, and expanded at the tip. These characteristics distinguish it from the condition seen in the taxa above and indicates
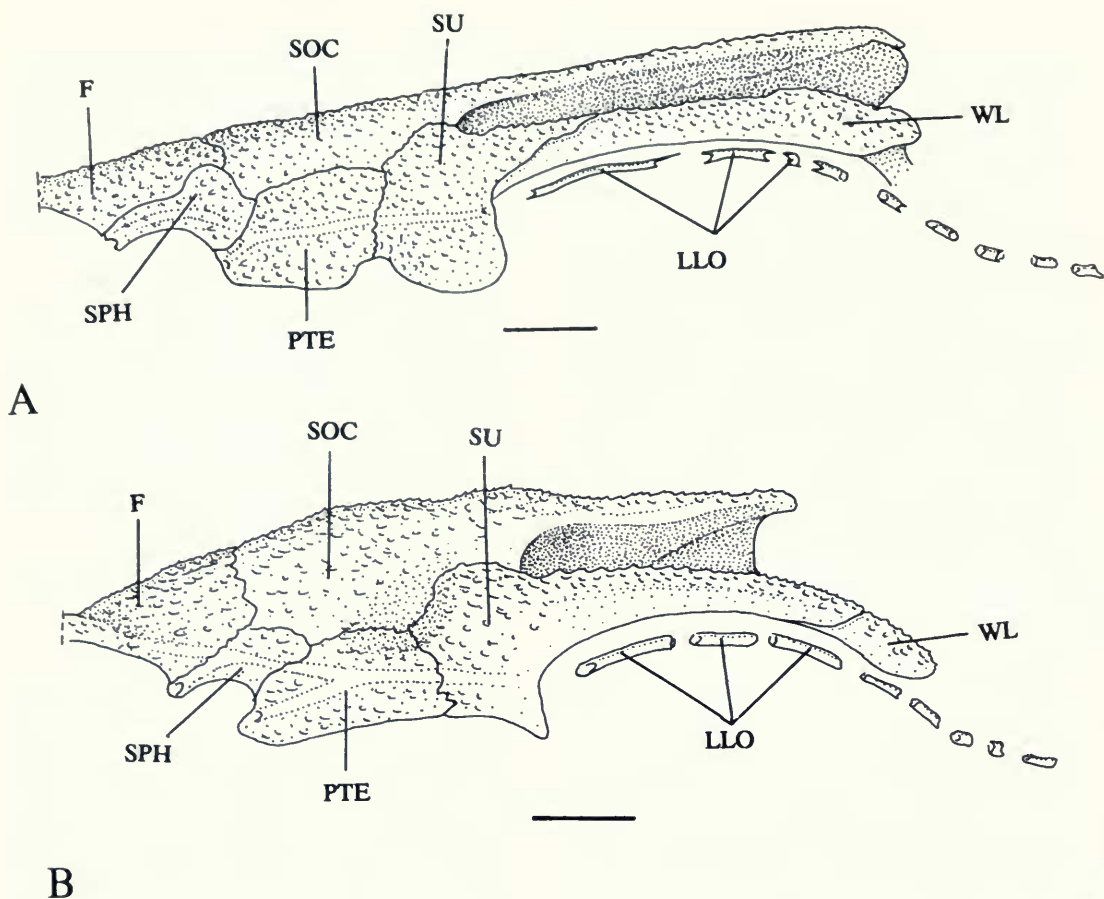
Fig. 11. Posterior portion of skull, Weberian lamina and lateral-line canal, lateral view. **A**, *Conta conta*, UMMZ 208632. **B**, *Erethistes pusillus*, UMMZ 208697. Scale bar = 1 mm.

nonhomology between the two structures, a conclusion also corroborated by the distant relative phylogenetic position of sisorids and doradoids within siluriforms (de Pinna, 1993).

30. Lateral ethmoid with narrow lateral extensions directed posteriorly alongside lateral margin of frontals (CI = 100, RI = 100).

Bagarius, [*Gagata* = ?], glyptosternoids, *Glyptothorax,* [*Nangra* = ?], *Pseudecheneis,* [*Sisor* = ?].

The dorsolateral portion of the lateral ethmoid in catfishes is frequently somewhat extended posteriorly underneath the lateral margin of the frontal. This extension is broad and not markedly differentiated from the body of the lateral ethmoid. Also, it normally does not extend along the level of the dorsal surface of the skull but instead is located ventral to the frontal. In the derived condition, the lateral ethmoids have long, narrow, posterior extensions running lateral to and at the same level as the frontals (Fig. 13). In many cases, the lateral ethmoid extensions form part or the whole of an antorbital process, and in glyptosternoids the extension can be considerably wider posteriorly. Although this was not observed in any specimens examined, it seems that the distal portion of the lateral ethmoid extensions may become detached in *Glyptosternum,* as observed by Tilak (1963, p. 289, Figs. 41, 42) and Gauba (1969, p. 3, Figs. 1, 14). Both authors considered the detached posterior piece an independent bone of unknown homologies. In view of the condition seen in related taxa, the independent structure probably originates by fragmentation from a portion of the lateral ethmoid. Some of the taxa above are coded as missing because of the extensive additional os-
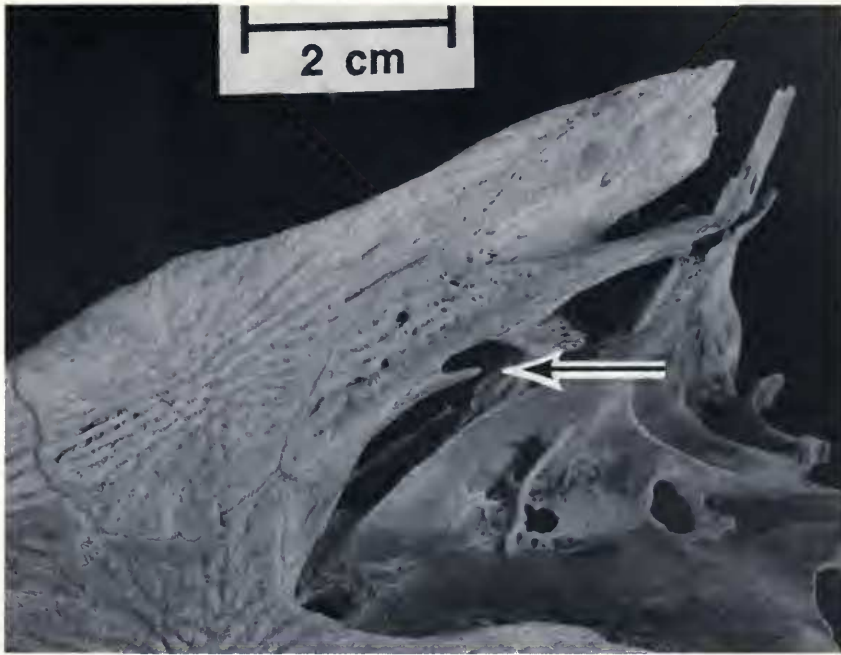
Fig. 12. *Bagarius yarrelli*, LACM 38294-55, posterior part of temporal region, dorsolateral view. Arrow indicates posterior process on epioccipital. Scale bar = 1 mm.

sification in the ethmoid region, which makes it difficult to observe the limit between certain regions of the frontal and lateral ethmoid.

31. Lateral processes of vomer long and thin, extending underneath entire length of articular processes of lateral ethmoid (CI = 100).

Glyptothorax.

The posterolaterally directed processes of the vomer give the bone its characteristic arrow shape in catfishes. Normally the processes are relatively short, not extending beyond the width of the ethmoidal region of the neurocranium. In all examined representatives of *Glyptothorax*, the vomer's processes are elongate and reach or nearly reach the tip of the articular process (which is itself quite elongated laterally, cf. character 32) of the lateral ethmoid (Fig. 14).

32. Articular region of lateral ethmoid an elongate process, with articular facet for palatine at tip (CI = 100, RI = 100).

Acrochordonichthys, Akysis, Breitensteinia, Par-

akysis, Amblyceps, Liobagrus, Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids, *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

The articulation for the palatine on the lateral ethmoid in siluriforms shows a well-defined articular facet provided with a cartilage lining continuous with the ethmoidal cartilage. Although the articular facet is well differentiated from the remainder of the lateral ethmoid, it does not extend markedly beyond the lateral margin of the bone. In the taxa above, which include all terminals treated in this analysis, in the articular region of the lateral ethmoid there is a long process extending directly lateral from the bone (Figs. 10, 13, 14). The articular facet for the palatine is located at the tip of that process. The plug of cartilage lining that facet is typically completely independent from the median ethmoidal cartilage in most taxa. The only taxa in which they are continuous are *Pseudecheneis* and perhaps *Gagata* (not clear in the material available). In *Nangra*, the two cartilages are almost continuous, separated only by a small gap. Based on the results of this analysis, the separation of cartilages is at the same phylogenetic level as the
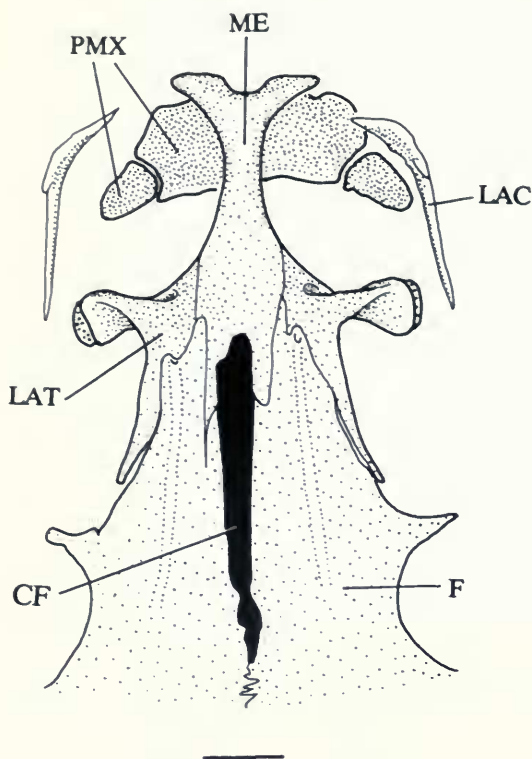
Fig. 13. *Glyptothorax major,* AMNH 58410, anterior part of skull and associated structures, dorsal view. Scale bar = 1 mm.

Fig. 14. *Glyptothorax sinensis,* AMNH 10265, anterior part of neurocranium, ventral view. Larger stippling represents cartilage. Scale bar = 1 mm.

elongation of the articular process, and conditions such as in *Pseudecheneis* are hypothesized to be reversals. Possibly, the elongation of the process and the separation of its distal cartilage from the main ethmoidal cartilage are two separate characters. However, until more information is available on the development of this complex in sisoroids and other catfishes, they are here conservatively treated as a single trait.

33. Mesethmoid cornua with dorsal subdivision (CI = 100, RI = 100).

Acrochordonichthys, Breitensteinia.

Primitively, the mesethmoid cornua in siluriforms are simple rod-like structures lacking noteworthy irregularities or deviations from their even surface. In these two genera, the mesethmoid cornua have a short subdivision stemming from their dorsal surface (Fig. 10). This dorsal "arm" is very
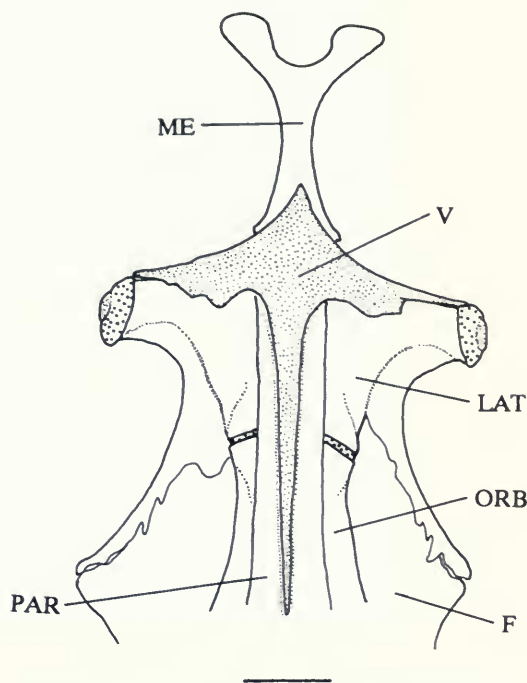
short and in some cases appears just as a swelling of the distal portion of the dorsal surface of the cornua.

34. Lateral ethmoid with well-defined dorsal facet contacting ventral surface of frontal (CI = 100, RI = 100).

Gagata, Nangra.

In the plesiomorphic condition, the contact between the lateral ethmoid and the frontal in siluriforms is made by simple flat surfaces on both bones. Uniquely, in *Gagata* and *Nangra,* the posterior region of the dorsal surface of the lateral ethmoid has a well-defined arc-shaped facet (Fig. 15) abutting the ventral surface of the frontal. This facet (herein called the dorsal facet of lateral ethmoid) is provided with a well-developed cartilage, clearly visible through the transparent frontal in counterstained specimens of thinly ossified species such as *Nangra nangra* and *Gagata cenia.* In species with heavily ossified skulls, the facet and its cartilage can be exposed by removing the anterior
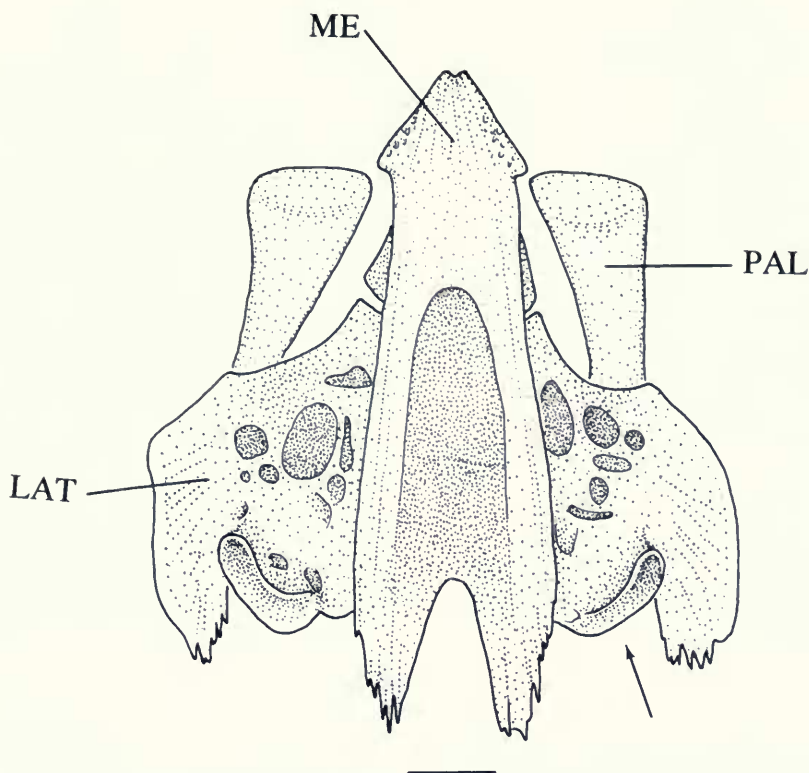
FIG. 15. *Gagata gagata,* AMNH 8358, ethmoid region, frontals removed, dorsal view. Arrow indicates dorsal facet on lateral ethmoid. Scale bar = 1 mm.

portion of the frontals. The cartilage of the facet is completely independent from the more ventrally located ethmoid cartilage.

The frontal facet of the lateral ethmoid is an extremely peculiar structure, without parallel in any other siluriform and probably unique among ostariophysans. Its functional significance is as yet unsolved; there seem to be no associated modifications in the frontal and no special bone movement in the region.

35. Lateral ethmoid cartilage for palatine facet with extension for lacrimal (CI = 100, RI = 100).

Gagata, Nangra.

The cartilage on the lateral ethmoid that connects it with the palatine is primitively restricted to this articulation. In the two genera above, this cartilage has a lateral extension of its dorsal margin that abuts the lateral surface of the lacrimal.

36. Sphenotic not contacting supraoccipital (CI = 100).

Pseudecheneis.

In most siluriforms and other ostariophysans, the sphenotic contacts posteromesially the anterolateral margin of the supraoccipital. Uniquely in *Pseudecheneis,* the two bones are separated by the frontal, which has a large posterior extension in that genus (Gauba, 1968, p. 233).

Branchial Arches

37. Last hypobranchial with anterolateral extension (CI = 100, RI = 100).

Conta, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia.

The anterolateral corner of the last (third) hypobranchial in catfishes is either similar in form
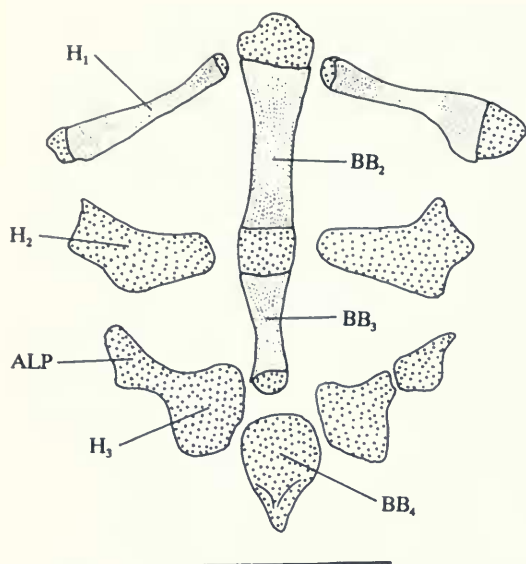
FIG. 16. *Erethistoides montana,* UMMZ 208745, basal portion of gill arches, dorsal view. Larger stippling represents cartilage. Scale bar = 1 mm.
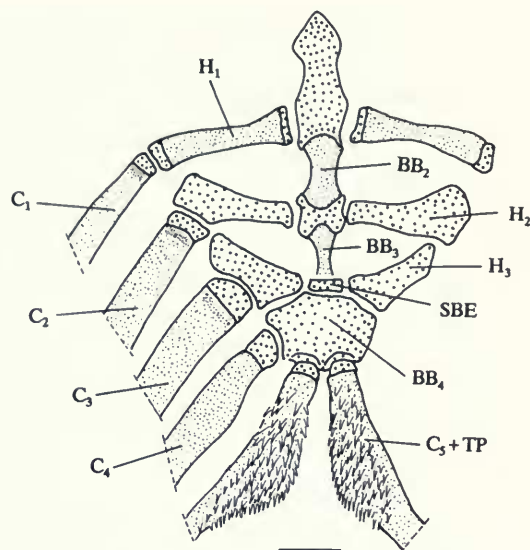

FIG. 17. *Acrochordonichthys ichnosoma,* MZUSP 42468, ventral portion of gill arches, dorsal view, gill rakers not represented. Larger stippling represents cartilage. Scale bar = 1 mm.

to the other corners of the structure or protrudes only slightly anterolaterally. In the taxa above, the third hypobranchial is strongly defined anterolaterally, and its anterolateral corner is modified into a large process (Fig. 16). In some cases the extension appears as an almost or distinctly separate cartilaginous element, as in *Erethistoides.*

38. Second hypobranchial unossified (CI = 50, RI = 88).

Acrochordonichthys, Breitensteinia, Parakysis, Conta, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia, Aspredinidae.

Primitively in catfishes, the first and second hypobranchials are ossified and the third is cartilaginous. The degree of ossification varies, and there is always a remnant cartilaginous rim posteriorly or at the tips of the ossified hypobranchials. In some instances, such as in some trichomycterids, the third hypobranchial is also ossified, a condition that approaches the state seen in nonsiluriform outgroups but that is derived within the order. In the taxa above, there is an apomorphic modification in the opposite direction, with only the first hypobranchial being ossified (Figs. 16, 17). Both the second and third hypobranchial are entirely cartilaginous, even in the adults examined.

In some specimens of *Laguvia ribeiroi,* there is a small ossified area on the second hypobranchial, which is interpreted here as an abnormality.

39. First hypobranchial unossified (CI = 100.)

Parakysis.

The first hypobranchial in catfishes is primitively ossified (see character 38). In *Parakysis,* the structure (as well as the other hypobranchials) remains cartilaginous in adults. Hypobranchials also fail to ossify in hoplomyzontin aspredinids. Although a phylogeny of aspredinids is not yet available, the condition in hoplomyzontins is tentatively interpreted as a result of paedomorphosis found exclusively in that tribe and thus is not representative of the general condition in aspredinids. All other members of the family retain the ossified condition for the first hypobranchial.

40. All basibranchials unossified (CI = 100, RI = 100).

Parakysis, [glyptosternoids = ?].

There is a large variation in the size and extent of basibranchial ossifications in siluriforms. Nearly always, however, there is some degree of ossi-

fication of the first and second basibranchial elements, a condition that can be considered plesiomorphic for the order. The third basibranchial is invariably cartilaginous in catfishes. In *Parakysis,* all basibranchial elements are present, but none are ossified. A similar condition is seen elsewhere only in *Oreoglanis* (in no other glyptosternoids). Therefore, glyptosternoids are coded as missing for this character. The conditions in *Parakysis* and *Oreoglanis* are quite different structurally. In *Parakysis* the cartilaginous basibranchials are of normal shape, whereas in *Oreoglanis* they are extremely narrow and elongate, nearly threadlike. Within aspredinids, basibranchial ossifications are very reduced or absent in hoplomyzontins. These reductions are postulated to be the result of the paedomorphic nature of that tribe and probably are not representative of the general condition in aspredinids. This assumption of nonhomology is supported by the overall phylogeny.

41. Additional cartilaginous element anterior to last basibranchial (CI = 20, RI = 50).

Acrochordonichthys, Breitensteinia, Parakysis, Bagarius, Glyptothorax, Laguvia, Pseudecheneis, Pseudolaguvia, Sisor.

The last basibranchial in siluriforms (the third from the anterior, homologous to the fourth in other ostariophysans) is a single cartilaginous structure that is usually much wider than the first and second basibranchials and is normally located immediately posterior to the latter. In the taxa above, there is a distinct separate cartilaginous element between the second and third basibranchials (Figs. 17, 18). This structure is most developed in *Acrochordonichthys rugosus* and *Breitensteinia insignis,* where it has the shape of a narrow rectangle closely addressed to the anterior margin of the third basibranchial. This supernumerary cartilage probably is formed as an anterior segmentation of the third basibranchial, insofar as it is usually more closely connected with the third rather than second basibranchial. Also, its width normally matches that of the broad third basibranchial instead of the much narrower second. In some cases, the extra cartilage is present in an extremely reduced condition, represented by a small globule of cartilage somewhat loosely situated between the second and third basibranchials. Such is the case in *Sisor* and *Laguvia.* The cartilage is present in most *Glyptothorax* except *G. pectinopterus.* Until more details are available on the development and structure of this cartilage, its
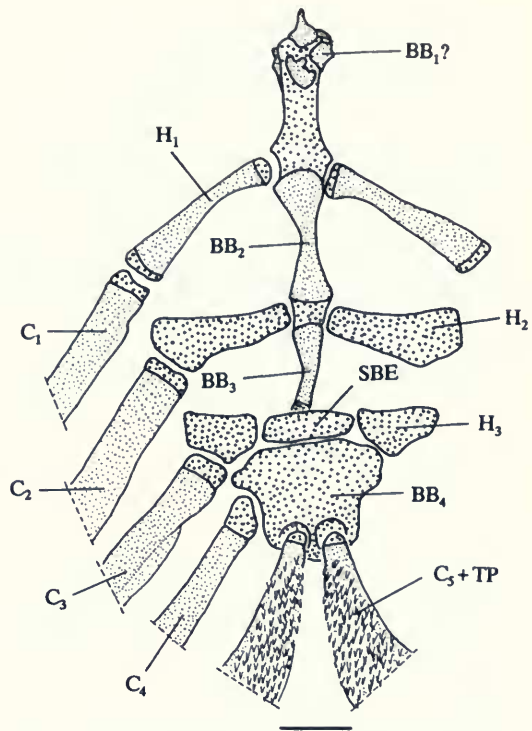

FIG. 18. *Breitensteinia insignis,* AMNH 58378, ventral portion of gill arches, dorsal view, gill rakers not represented. Larger stippling represents cartilage. Scale bar = 1 mm.

variation in shape and size cannot be utilized as primary evidence for relationships. Its presence, however, can justifiably be hypothesized as derived.

42. First epibranchial expanded anteriorly (CI = 100).

Pseudecheneis.

The first epibranchial in siluriforms is primitively round or flat in cross-section and not markedly wider in dorsal view than the more posterior second and third epibranchials. Uniquely, in *Pseudecheneis,* the first epibranchial is broad, roughly three times as wide as the second epibranchial.

43. Second hypobranchials with longest axis nearly perpendicular to first (CI = 100, RI = 100).

Amblyceps, Liobagrus.

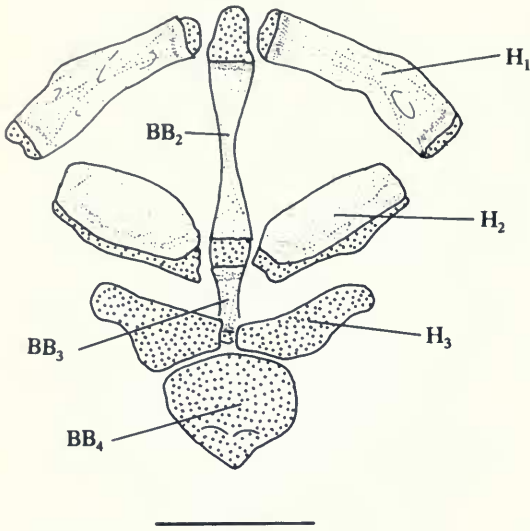The margins of first and second hypobranchials in catfishes are usually parallel or slightly divergent

FIG. 19. *Amblyceps mangois*, ANSP 59316, basal portion of gill arches, dorsal view. Larger stippling represents cartilage. Scale bar = 1 mm.
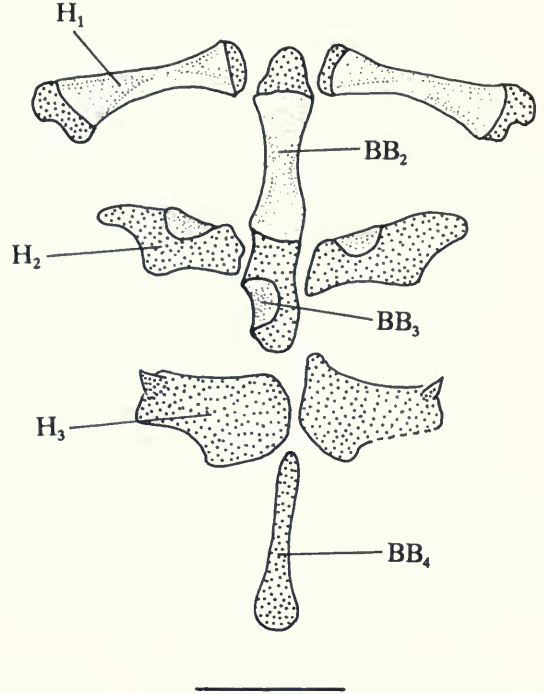

FIG. 20. *Sisor rhabdophorus*, BMNH 1970.6.25.1, basal portion of gill arches, dorsal view. Larger stippling represents cartilage. Scale bar = 1 mm.

mesiad. In amblycipitids, the two bones (i.e., the posterior margin of first and anterior margin of second hypobranchials) diverge strongly toward the midline, forming a nearly 90° angle mesially (Fig. 19). This peculiar relative position seems to be the result of a shift in the orientation of the second rather than the first hypobranchial.

44. Last basibranchial narrow (CI = 50, RI = 0).

Gagata, Sisor.

The last basibranchial in catfishes is always unossified and primitively is considerably wider and rounder in dorsal view than are the two more anterior basibranchials. In *Sisor* and *Gagata,* the last basibranchial is apomorphically modified into a long and thin cartilage, as narrow as or more so than the more anterior basibranchials (Fig. 20). The narrowing does not affect the vertical component of the cartilage, which remains as deep (in lateral view) as in the plesiomorphic condition. The condition is most extreme in *Sisor.*

45. Anterior cartilage of anteriormost basibranchial enlarged (CI = 50, RI = 50).

Acrochordonichthys, Akysis, Breitensteinia.

The first basibranchial of other ostariophysans is absent in siluriforms. Their anteriormost basi-

branchial (corresponding to the second in other otophysans) has an anterior rim of cartilage that articulates with the mesial ends of the first pair of hypobranchials. In the taxa above, the anterior cartilage of the second basibranchial is elongated anteriorly, reaching beyond the anterior margin of the hyoid bar (Figs. 17, 18). The enlarged cartilage sometimes shows some irregular areas of ossification, such as in *Breitensteinia* (Fig. 18). It is unclear if this cartilage represents an atavistic expression of the first basibranchial of nonsiluriform ostariophysans.

45. Fourth ceratobranchial with tooth plates (CI = 100).

Bagarius.

In siluriforms, only the fifth ceratobranchial typically bears tooth plates. Almost uniquely within the order, *Bagarius* possesses narrow tooth plates attached also along the dorsal border of its fourth ceratobranchial. These tooth plates are absent in

the fourth ceratobranchials of the largest specimen examined of the genus (a member of *B. yarrelli*) but are present in smaller specimens of the same species. The tooth plates may have been lost in that specimen (which is a dry skeleton and therefore more prone to tooth plate detachment), or alternatively they may disappear with growth. Gauba (1962) did not describe or illustrate tooth plates on the fourth ceratobranchial of *Bagarius bagarius*. It is unclear whether their absence therein was due to large size because the size of specimens examined is not indicated in the paper.

47. Lateral cartilage of first hypobranchial enlarged (CI = 100).

Aspredinidae.

The lateral cartilage of the first hypobranchial in siluriforms is primitively far shorter than the bony portion of the bone. In the derived condition, the cartilage is at least 50% of the length of the bony portion of the first hypobranchial. This character could not be observed in the specimens of hoplomyzontins examined because their first hypobranchials are unossified and reduced or absent.

48. Last basibranchial bifurcated anteriorly (CI = 100).

Pseudolaguvia.

The totally cartilaginous last basibranchial in catfishes is undivided anteriorly in the plesiomorphic state. In *Pseudolaguvia*, the basibranchial is anteriorly split into two short arms, with their tips slightly expanded and curved laterally.

49. Proximal portion of first and/or second epibranchial curved posteriorly (CI = 50, RI = 66).

Glyptosternoids, *Glyptothorax,* [*Laguvia* = ?], *Pseudecheneis, Pseudolaguvia.*

The first and second epibranchials in siluriforms are roughly straight in the plesiomorphic condition. In the taxa above, the proximal portions of the first or second epibranchials (or more frequently both) are strongly curved posteriorly. The change in direction may be a distinctly angled twist, as in *Glyptothorax,* or a more gentle curve, as in *Pseudecheneis* and glyptosternoids. The condition in *Laguvia* is weakly developed and in some specimens is similar to the plesiomorphic condition.

50. Proximal portions of epibranchials 1 and 2 adpressed to one another (CI = 100).

Bagarius.

The first and second epibranchials in catfishes are primitively not particularly close to each other, being connected by connective tissue in a way comparable to that between other epibranchials. In *Bagarius,* the first and second epibranchials are closely adpressed along their proximal margins. The two bones are furthermore anteroposteriorly flattened at the area of connection, increasing the surface of contact.

Hyoid Bar

51. Branchiostegal rays forming a closed round arrangement (CI = 100, RI = 100).

Amblyceps, Liobagrus.

The angular difference between the bases of the first and last branchiostegal rays in catfishes is primitively about 90°. In the taxa above, the bases of the first and last branchiostegal rays are oriented approximately at a 135° angle to one another. This orientation results in a peculiar arrangement in which the set of branchiostegal rays in amblycipitids surrounds a major portion of the posterior margin of the hyoid bar.

52. Lateral wings of urohyal extremely reduced or absent (CI = 100, RI = 100).

Glyptosternoids, *Glyptothorax, Pseudecheneis.*

The urohyal in siluriforms primitively has bilateral laminar expansions in the form of lateral "wings" extending from the margins of a relatively small central body (Arratia & Schultze, 1990). In the taxa above, the urohyal is composed mostly of the narrow median portion, with the wing-like extensions small or totally absent (Fig. 21).

53. Proximal end of anterior ceratohyal with narrow, anterolaterally directed extension (CI = 100, RI = 100).

Acrochordonichthys, Breitensteinia.

The mesial end of the anterior ceratohyal in catfishes is primitively a simple structure, roughly rounded in cross-section at its articulation with the hypohyal and without major expansions or
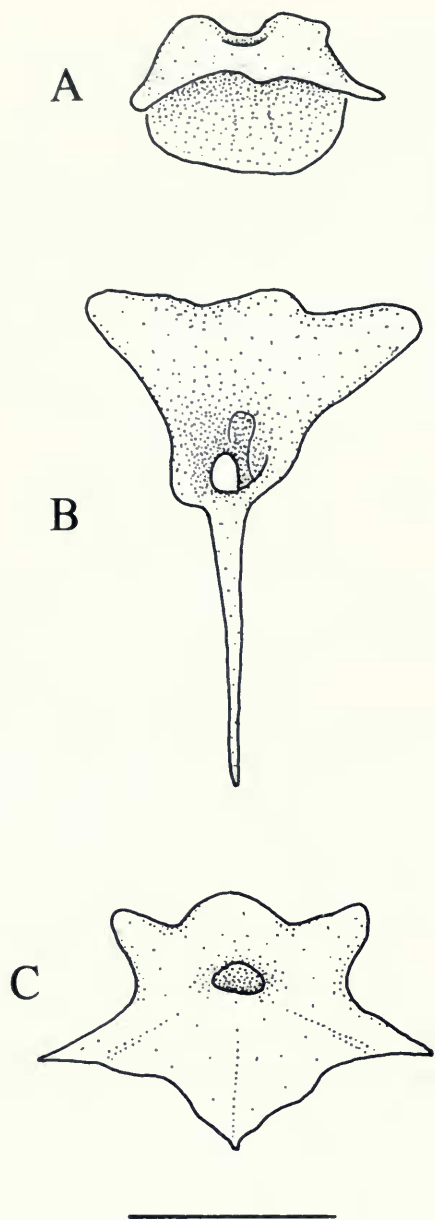
FIG. 21. Urohyals in ventral view. **A**, *Glyptothorax sinensis*, AMNH 10265. **B**, *Exostoma* sp., USNM 130183. **C**, *Pseudecheneis sulcatus*, BMNH 1985.9.16:50. Scale bar = 1 mm.

processes. In the taxa above, the anterior margin of the proximal end of the anterior ceratohyal is developed into a narrow, anterolaterally oriented process (Fig. 22). The process does not involve any portion of the articular surface for the hypohyal and is devoid of cartilage. The hypohyal in

some species has an equivalent process laterally, which is ankylosed to the anterior process of the ceratohyal. A similar structure also occurs in a single glyptosternoid examined, *Pseudexostoma*. In that genus, however, the condition differs in that the process includes part of the articular surface for the hypohyal and is accordingly lined with cartilage along its anterior margin. This morphological difference, plus the fact that all other glyptosternoids lack the derived condition, indicates that the condition in *Pseudexostoma* is not homologous to that of *Breitensteinia* and *Acrochordonichthys*.

54. Posterior margin of anterior ceratohyal with laminar expansion forming laterally directed process (CI = 100, RI = 100).

Conta, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia.

The plesiomorphic condition for the anterior ceratohyal in catfishes is to have the form of a simple bar somewhat expanded vertically in its anterior and posterior portions and roughly round or triangular in cross-section. In the taxa above, the anterior ceratohyal has a posterior laminar shelf with irregular margins (Fig. 23). The extent of the shelf varies, and in extreme cases it extends along the entire posterior margin of the bone. Laterally, the shelf has a large concavity that delimits a broad, laterally directed process. The structure can be markedly reduced in some species of the genus *Laguvia* but is well developed in the closely related *Pseudolaguvia*.

55. Posterior ceratohyal with dorsal process near its connection with suspensorium (CI = 100, RI = 100).

Acrochordonichthys, Breitensteinia, Parakysis.

The proximal tip of the posterior ceratohyal in siluriforms primitively has an irregular surface, with small depressions at the sites of ligament attachment. The region next to the dorsal tip of the bone lacks any well-differentiated processes. In the derived condition, there is a prominent process on the dorsal margin of the posterior ceratohyal immediately dorsal to its distal tip (Fig. 22). This process, which is apparently not an attachment site for the ligamentous connections between the hyoid bar and the mesial surface of the suspensorium, is most developed in *Acrochordonichthys* and *Breitensteinia*.
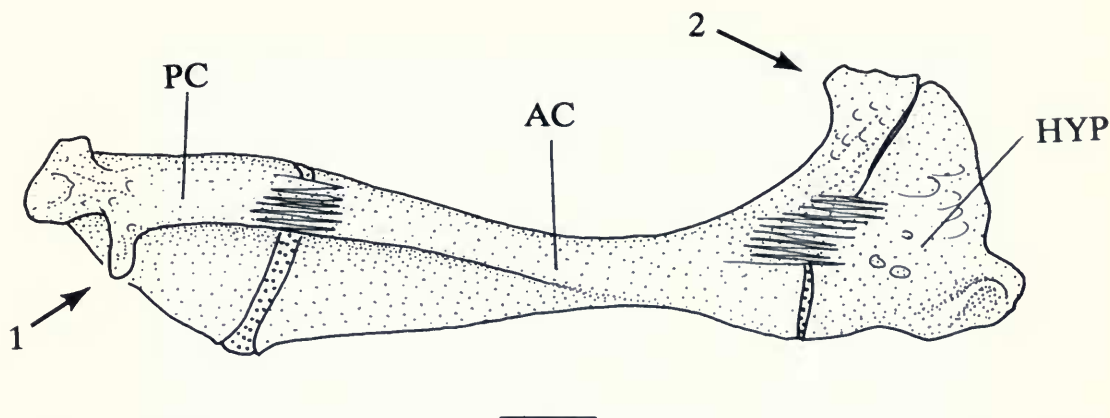
FIG. 22. *Breitensteinia insignis,* AMNH 58378, hyoid bar, dorsal view. Arrow 1 indicates dorsal process on posterior ceratohyal; arrow 2 indicates anterior expansion of anterior ceratohyal. Larger stippling represents cartilage. Scale bar = 1 mm.

Weberian Apparatus

56. Weberian capsule complete, without apparent lines of suture (CI = 100, RI = 100).

Gagata, Nangra, Sisor.

The Weberian complex in siluriforms has a number of different forms of swim bladder encapsulation. They all usually involve some degree of wrapping of the swim bladder by the parapophyses of the complex centrum (Alexander, 1965). In several taxa, there is also a contribution to the ventral wall of the capsule by neomorph offshoots of the ventral surface of the complex centrum. In any case, the walls of the bony capsule contain gaps or lines of suture between its different components. In the taxa above, in contrast, the capsule is continuous and surrounds the whole swim bladder (except its lateral surface) without spaces or trace of sutures (Fig. 24). Elsewhere in siluriforms, a similar capsule morphology is found in Neotropical loricarioids and in *Leptoglanis* and *Zaireichthys* of the African Amphiliidae. In view of the number of nodes separating loricarioids from sisorids with encapsulated swim bladders in the hypothesized phylogeny of siluriforms (de Pinna, 1993), the conditions in loricarioids and in some sisorids are assumed to be independent. A similar
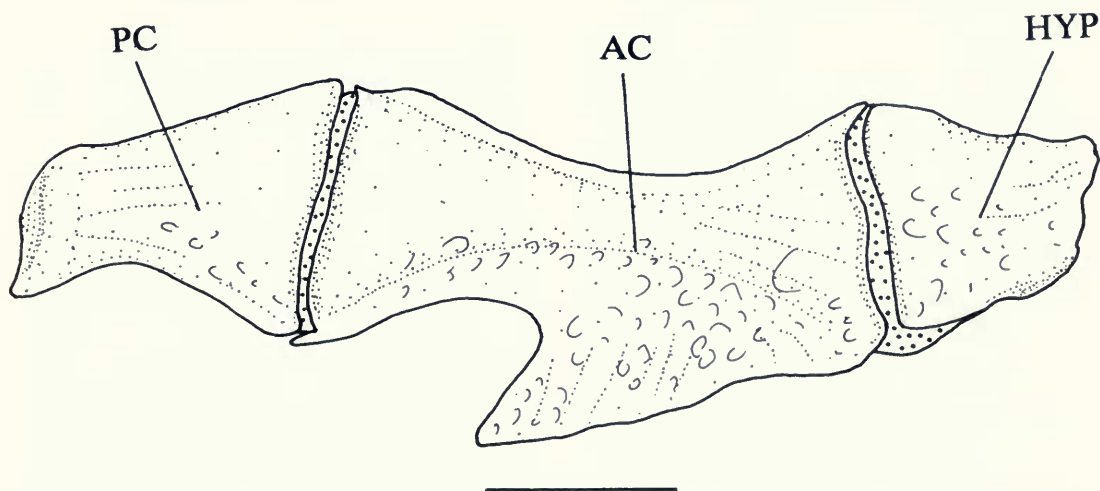

FIG. 23. *Hara hara,* UMMZ 208748, hyoid bar, dorsal view. Larger stippling represents cartilage. Scale bar = 1 mm.
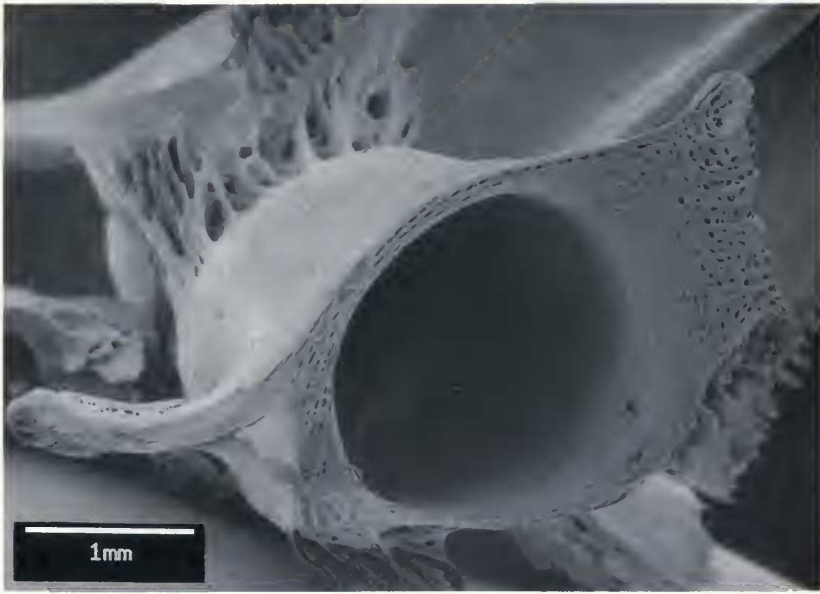
Fig. 24. *Gagata gagata*, AMNH 8358, SEM photograph, ventrolateral view of swim bladder capsule.

reasoning applies to *Leptoglanis* and *Zaireichthys,* which are demonstrably closer to other amphiliids than to any sisorids (de Pinna, 1993).

57. Parapophysis of fifth vertebra strongly flattened and expanded (CI = 50, RI = 87).

Bagarius, Conta, Erethistes, Erethistoides, Gagata, Glyptothorax, Hara, Laguvia, Nangra, Pseudolaguvia, Sisor, Aspredinidae.

The parapophysis of the fifth vertebra in catfishes is primitively a narrow structure, often gently curved anteriorly, that tapers toward a pointed tip. In the taxa above, the parapophysis is modified into a stout shelf-like structure, often markedly expanded horizontally toward its distal end (Fig. 25, 26). In *Gagata,* the parapophysis is partly incorporated into the swim bladder capsule and is somewhat reduced. However, it still clearly corresponds to the derived condition.

58. Parapophysis of fifth vertebra branched or notched distally (CI = 100, RI = 100).

Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia, [Aspredinidae = ?].

In the taxa above, the fifth parapophysis, besides being expanded laterally, is notched one or more

times along its distal margin (Fig. 26B). In the more extreme forms, the notching is deep and multiple, forming a coarse branching of the flat distal portion of the parapophysis. Within aspredinids, the process is notched in Bunocephalini and some members of Hoplomyzontini, but not in Aspredininae. Because the family is treated as a single terminal for this analysis, this character is coded as missing for this family.

59. Complex centrum as short as or shorter than free centra (CI = 100, RI = 100).

Glyptosternoids, *Pseudecheneis.*

The complex centrum of siluriforms, composed of fused primitive centra 2–4, is considerably shorter than the summed lengths of three free centra, indicating that considerable shortening has occurred along with the fusion process (Alexander, 1965). The shortened complex centrum, however, is primitively still longer than a single free centrum. In the derived condition observed for *Pseudecheneis* and glyptosternoids, the complex centrum is shortened to an extreme degree, being as short as or shorter than the individual free centra immediately posterior to it.
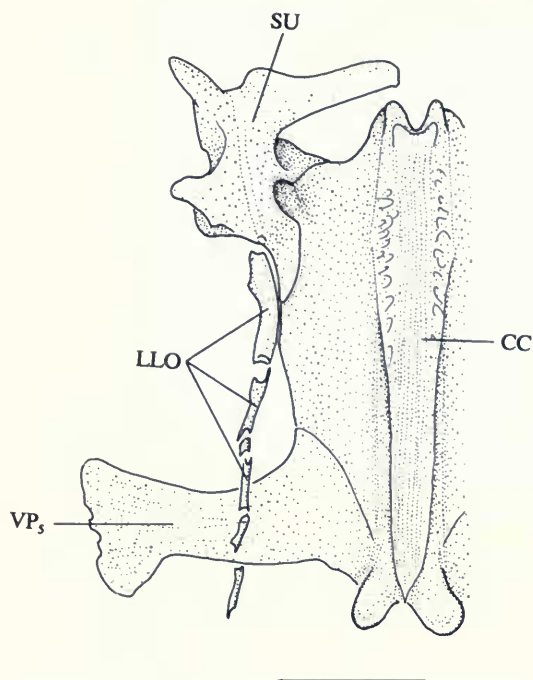
FIG. 25. *Dysichthys coracoideus,* AMNH 21815, dorsal (partial) view of Weberian complex, supracleithrum, and part of lateral line; anterior on top. Scale bar = 5 mm.

FIG. 26. Ventral view of Weberian complex. **A,** *Glyptothorax major,* AMNH 58410. **B,** *Laguvia ribeiroi,* UMMZ 208955. Scale bar = 1 mm.

60. Distal tip of os suspensorium closely linked and/or adpressed to ventral process of complex centrum (CI = 100, RI = 100).

Bagarius, Gagata, glyptosternoids, *Glyptothorax, Nangra, Pseudecheneis, Sisor.*

The distal tip of the os suspensorium in siluriforms is primitively free from any direct contact or strong ligamentous connections with a bony surface other than for the transformator process of the tripus. In the taxa above, the os suspensorium is firmly linked to the independent process that underlies part of the ventral wall of the swim bladder (Fig. 26A). In some taxa, the two structures almost form a single shelf, although actual fusion is not observed except in taxa with a complete swim bladder capsule, namely *Nangra, Gagata,* and *Sisor.* Here the ventral process of the compound centrum is indistinguishably fused to the Weberian lamina, forming a complete swim bladder capsule. The os suspensorium in these cases seems to be modified or incorporated into a thick strut of bone fused dorsally to the internal wall of the capsule (Fig. 27). This condition is assumed to be a modification of the connection observed in the remaining taxa listed above.
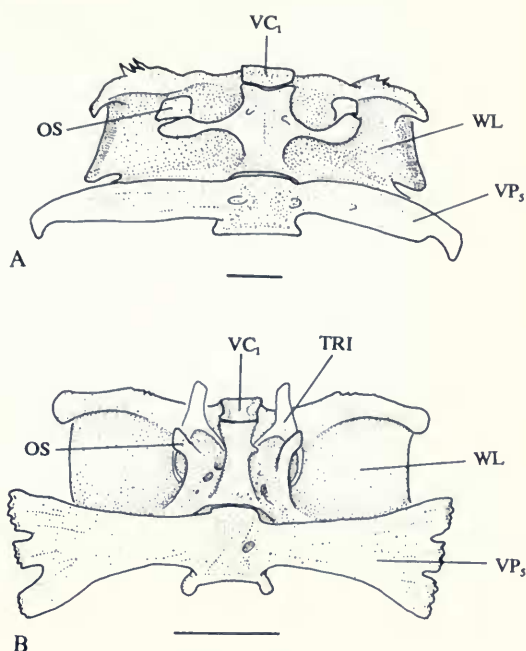
61. Parapophysis of fifth vertebra strong and attached to ventral side of centrum, directed directly perpendicular to vertebral axis (CI = 100).

All terminal taxa.

The parapophysis of the fifth vertebra in catfishes is primitively a narrow laminar structure attached to the dorsal half of its centrum and usually gently curved anteriorly. In the derived condition, the base of the parapophysis is located on the ventral half of the centrum, is not laminar, and is directed straight laterally. There is a significant amount of phylogenetically informative variation in the morphology of this parapophysis, and its size ranges from very short (as in amblycipitids and akysids) to very long so as to reach the body wall laterally (as in aspredinids and many sisorids). These similarities indicate, however, that some of the modifications are homologous throughout all terminal taxa included in this analysis. This par-

FIG. 27. *Gagata gagata*, AMNH 8358, SEM photograph, tripus, lateral view inside capsule shown in Figure 24.

apophysis is sometimes referred to as a transverse process (e.g., Chardon, 1968). However, transverse process has been used in this and other works to refer to a different vertebral structure (cf. character 70). The structure here called the parapophysis of the fifth vertebra appears to be serially homologous to a vertebral parapophysis. In support of that conclusion, half-grown specimens of *Liobagrus anguillicaudatus* (AMNH 11069) have small pleural ribs associated with the modified parapophyses, in the position expected for normal vertebral parapophyses.

62. Parapophysis of fifth vertebra long, almost or quite reaching lateral surface of body wall (CI = 100, RI = 100).

Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids, *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

The parapophysis of the fifth vertebra in all terminals of this analysis is apomorphically modified from the condition observed in other siluriforms, as described for character 61. In all terminal taxa except akysids and amblycipitids, the parapophysis undergoes an additional modification in its length and extends laterally well beyond the limit of the parapophyses of the complex centrum (Figs. 25, 26). In most taxa, it extends laterally all the way to the body wall. In glyptosternoids, the complex centrum and associated structures are highly modified. Here, the parapophysis of the fifth centrum is markedly smaller and narrower than in other members of this clade and seems to be an extreme condition of the modifications seen in *Pseudecheneis,* the closest relative.

63. Posterodorsal corner of Weberian lamina with pointed process directed posteriorly (CI = 100, RI = 100).

Bagarius, Gagata, Nangra, Sisor.

The posterolateral corner of the Weberian lamina (modified parapophysis of complex centrum) in siluriforms is primitively a simple angle without conspicuous processes or expansions. Sometimes there is a small thickening of bone that does not form a well-differentiated structure. In the taxa above, there is a thick and well-defined process on the posterolateral corner of the lamina, directed posteriorly and frequently ornamented on its lateral surface (Fig. 24). In all the taxa above except *Bagarius,* the lamina is modified to form the posteroventral portion of a swim bladder capsule, but the process remains well differentiated and departs markedly from the lateral margin of the capsule. In *Bagarius,* the process is well developed in small to medium-sized individuals but seems to get less defined with growth.
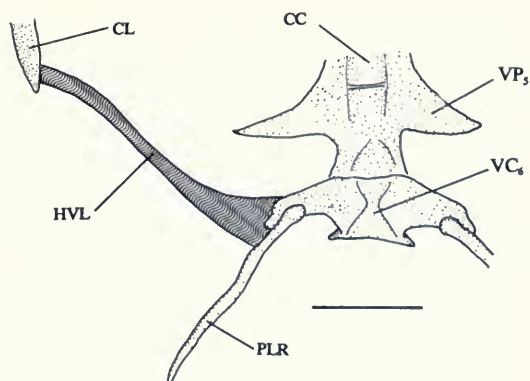
Fig. 28. *Akysis* sp. 1, UMMZ 214907, anterior portion of vertebral column, right humerovertebral ligament and tip of right humeral process, ventral view. Wavy lines represent ligament. Scale bar = 1 mm.
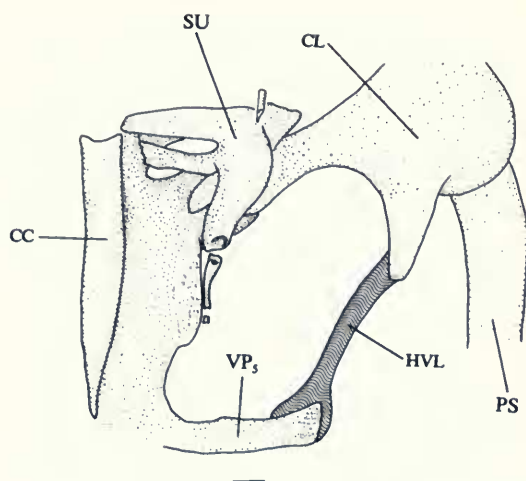

Fig. 29. *Amaralia hypsiura,* AMNH uncat., part of Weberian complex, right humerovertebral ligament, supracleithrum, and part of pectoral girdle, dorsal view. Wavy lines represent ligament. Scale bar = 1 mm.

64. Humeral region connected with anterior portion of vertebral column by well-defined ligament (humerovertebral ligament) (CI = 60, RI = 60).
    State 1: *Amblyceps, Liobagrus.*
    State 2: *Acrochordonichthys, Akysis, Breitensteinia.*
    State 3: *Bagarius, Conta, Erethistes, Erethistoides, Gagata, Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae. [*Parakysis* = ?].

The humeral process in catfishes is a stout, pointed process directed posteriorly on the upper limb of the cleithrum. It primitively lacks well-defined ligamentous connections with surrounding skeletal elements. In the derived condition displayed by the taxa above, the tip of the humeral process (or the soft tissue in the vicinity of the humeral region) is linked to the vertebral column by a conspicuous ligament (Figs. 28, 29). This ligament, here named the humerovertebral ligament, is most evident in aspredinids. There are three well-defined conditions of the attachment of the ligament on the vertebral column, distinguished by a number of traits. In the first (state 1), the ligament attaches posteriorly on either the parapophysis or the rib of the sixth vertebra and anteriorly ends in soft tissue (seemingly associated with the wall of the axillary gland, but this association could not be verified with certainty in the preparations available) without actually reaching the humeral process or any other bone. In the second condition (state 2), the ligament is ante-

riorly firmly attached to the mesial surface of the tip of the humeral process. Posteriorly it inserts on the lateral side of the sixth vertebral parapophysis and proximal portion of its corresponding rib (Fig. 28). In a few taxa (e.g., *Akysis* sp. 2), part of the ligament also attaches on the fifth parapophysis. In the third condition (state 3), the ligament attaches anteriorly on the humeral process, as in state 2, but its posterior attachment is exclusively on the ventral surface of the distal portion of the highly modified parapophysis of the fifth vertebra (Fig. 29). The attachment site on the parapophysis is usually delimited by some bony indentation on the anterior margin of the parapophysis.

The humerovertebral ligament varies widely in length, according to the distance between the tip of the humeral process and the vertebral attachment. At one extreme is the situation in *Bagarius,* where the two attachment sites are nearly juxtaposed and the ligament is consequently very short. The other extreme is exhibited in *Akysis,* where the ligament can be slightly longer than the longest pleural rib.

A humerovertebral ligament was not directly observed in the specimen of *Sisor* available because its preparation did not preserve ligaments in good condition. However, the anterior margin of its fifth vertebral parapophysis has a slight notch corresponding to the attachment site of the ligament in other taxa. On the basis of this, *Sisor* is

tentatively assigned state 3 for this character. This assumption should be verified in additional specimens of the genus when they become available.

Pseudecheneis, which lacks a humeral process, has a humerovertebral ligament attaching anteriorly onto a small cleithral splint immediately ventral to the articulation between the cleithrum and the skull. This splint is probably a remnant of the humeral process, which apparently in this taxon serves only as an attachment for the ligament. All other sisorid and akysid taxa that lack the humerovertebral ligament also lack the humeral process (e.g., glyptosternoids, *Parakysis*). This character is coded as missing for *Parakysis* because of the presence of a conspicuous vertebral ligament that cannot be unambiguously homologized with the humerovertebral ligament. This ligament unites the first pleural rib with the neural prezygapophysis of its own supporting vertebra, and it may arguably be a highly modified humerovertebral ligament. Resolution of this question will have to await examination of additional material and an ontogenetic series of *Parakysis,* currently unavailable.

It was not possible to determine the ordering of the three states defined above because there is no evident sequence from a less extreme to a more extreme condition. Also, no ontogenetic information relevant to the question is available. Therefore, the three states of the humerovertebral ligament are considered unordered (nonadditive) for the purpose of parsimony analysis. Thus, the transitions of the character are ambiguous on the most parsimonious topology, and in one possible optimization the three states are considered independently derived. This alternative is unrealistic because the presence of the ligament itself, being unique among catfishes, is obviously evidence for the monophyly of a large assemblage composed of all taxa above. Therefore, although the ordering of this character is presently unknown, it constitutes valid evidence for the monophyly of the whole group under study (see diagnoses for clades below), with two reversals to total absence (in *Parakysis* and glyptosternoids).

The very conspicuous humerovertebral ligament in *Aspredo* was first reported by Bridge and Haddon (1893, p. 185, Fig. 73). These authors, however, did not note its presence in their specimens of Akysidae and Sisoridae. Tilak (1963, p. 298) observed the presence of the humerovertebral ligament in the sisorids *Nangra, Glyptothorax,* and *Glyptosternum* but stated that it was absent in *Gagata* and *Bagarius.* This "absence" is likely an artifact of preservation, because a well-developed ligament is present in all representatives of *Gagata* and *Bagarius* examined. Chardon (1968) also described the humerovertebral ligament in sisorids (p. 127) and aspredinids (pp. 171, 173) and clearly illustrated the structure in representatives of Aspredinidae (cf. Chardon, 1968, Figs. 157–160). Chardon, however, did not comment on the possible significance of the sharing of this trait by the two taxa.

The functional significance of the humerovertebral ligament is rather obscure. It seems to restrict lateral movement of the anterior vertebrae relative to the pectoral girdle because the ligaments are disposed bilaterally as antagonists relative to the horizontal plane of the vertebral column. Movement in that plane, however, is already severely limited in catfishes in general by the nature of their pectoral suspension and the fusion involved in the formation of the complex centrum. Also, in several members of the ingroup, movement of the skull relative to the complex centrum is impossible because of the firm bony bridge formed by the supracleithrum between the back of the skull and the lateral margin of the Weberian lamina (cf. character 27). All these modifications seem to be part of a general trend toward reduction of movement of the anterior part of the body, including the Weberian complex, relative to the free portion of the vertebral column. The humerovertebral ligament may play an important role in the functioning of the stridulatory apparatus (cf. character 109 and discussion below on the evolution of the sound-producing apparatus).

65. Superficial ossification on ventral surface of complex centrum combined with part or all of os suspensorium, forming elongated anteroventral flange, anteriorly reaching basioccipital (CI = 100, RI = 100).

Erethistes, Hara.

In the plesiomorphic condition for siluriforms, the os suspensorium is a relatively narrow, flat, bony arc that extends anteroventrally in the space circumvented by the curvature of the transformator process of the tripus. Further, the os suspensorium has a mostly even width from base to tip, and its anteriormost point is free and distant from the basioccipital. In the derived condition, the distal portion of the os suspensorium fuses with the ventral superficial ossification of the complex centrum, and the resulting structure is expanded into a leaf-like flange distally adjoined but

not fused to the ventrolateral surface of the complex centrum. The anterior tip of the shelf reaches the basioccipital anteriorly. The degree to which the os suspensorium and the superficial ossification contribute to the final compound structure is unclear, although the superficial ossification seems to form a larger area of the leaf-like expansion. In some cases, a small protuberance of bone remains at the primitive site of the distal tip of the os suspensorium. Ossa suspensoria show comparatively modest morphological variation in catfishes, and the form seen in these taxa is one of the most remarkable modifications of this structure observed in the order.

66. Posterior part of Weberian lamina extensively contacting parapophysis of fifth vertebra (CI = 100, RI = 100).

Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids, *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

The posterior region of the Weberian lamina in siluriforms is primitively independent of the parapophysis of the fifth vertebra. It may approach the parapophysis and even contact its margin for a very short area near the vertebral centrum, but this contact is never extensive or firm. In the derived condition observed in all terminal taxa except amblycipitids and akysids, the Weberian lamina overlaps and broadly contacts the dorsal surface of the enlarged fifth parapophysis, and the two structures are either strongly connected or ankylosed.

67. Posterior portion of Weberian lamina with lateral extension along anterior margin of parapophysis of fifth vertebra (CI = 100, RI = 100).

Bagarius, Gagata, glyptosternoids, *Glyptothorax, Nangra, Pseudecheneis, Sisor.*

As described for character 66, the posterior part of the Weberian lamina is tightly and extensively connected to the dorsal surface of the parapophysis of the fifth vertebra, an apomorphic condition shared by all ingroup taxa except amblycipitids and akysids. In the subset listed above, there is a further modification of that derived condition, in which the posterior part of the Weberian lamina is laterally expanded to cover part or all of the anterior margin of the parapophysis of the fifth vertebra. In *Gagata,* the basal portion of the fifth

vertebral parapophysis is completely incorporated into the ventral wall of the swim bladder, with only its distal portion still independent (see character 69). A long suture is visible in this free portion, indicating the limit between the parapophysis itself and the apomorphic elongate lateral process of the Weberian lamina in other taxa.

68. Parapophysis of fifth vertebra with vertical lamina (CI = 100, RI = 100).

Erethistes, Hara.

The parapophysis of the fifth vertebra, which is enlarged in several members of the ingroup, is primitively a dorsoventrally flat horizontal shelf. In *Hara* and *Erethistes,* the parapophysis has a well-developed vertical wall dorsally continuous with and ankylosed to the posterior margin of the Weberian lamina. The condition is somewhat reduced, but still present, in the miniature *Hara jerdoni.*

69. Parapophysis of fifth vertebra incorporated into ventral wall of swim bladder capsule (CI = 100).

Gagata.

The parapophysis of the fifth vertebra is tightly united with the Weberian lamina in numerous members of the ingroup. The anterior margin of the parapophysis is adpressed to the posterior wall of the swim bladder capsule when this capsule is present, such as in *Nangra* and *Sisor.* In these cases, however, the parapophysis remains well differentiated from the capsule itself and is located posterior to it. Uniquely in *Gagata,* the parapophysis of the fifth vertebra in incorporated into the capsule to an extreme degree. Its proximal portion is indistinguishably fused to the ventral wall of the capsule.

Vertebrae and Ribs
(Other Than Weberian Apparatus)

70. Dorsal expansion on first pleural rib (CI = 100).

Pseudecheneis.

The pleural ribs in siluriforms are primitively a simple splint of bone, round or flat in cross-section. In *Pseudecheneis,* the flat first pleural rib has a large laminar expansion dorsally. The expansion
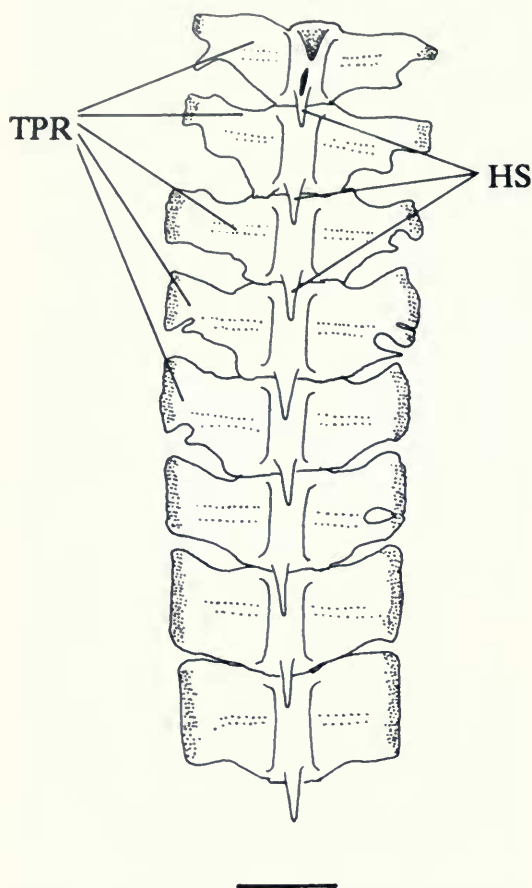
TPR

HS

FIG. 30. *Breitensteinia insignis*, AMNH 58378, part of vertebral column comprising free vertebrae 10–17, ventral view. Scale bar = 1 mm.

is broad-based and slightly hooked at its lateral tip.

71. Vertebral parapophyses sutured to one another (CI = 100).

Breitensteinia.

The vertebral parapophyses in catfishes, which are fused to their respective centra, are primitively separated from each other along the vertebral column. In *Breitensteinia*, the parapophyses are sutured to their neighbors at their anterior and posterior borders. These sutures seem to markedly limit the lateral movements of the vertebral column.

72. Vertebrae with transverse processes (CI = 33, RI = 50).

Acrochordonichthys, Breitensteinia, Parakysis, Sisor, Aspredinidae.

Vertebral transverse processes are lacking in most siluriforms, a plesiomorphic condition for the order. In the taxa above, a transverse process extends horizontally from the centrum of at least some caudal vertebrae (Fig. 30). These processes are considered neomorphs, not modified parapophyses, because some vertebrae have both structures. The maximum development of the processes is observed in *Breitensteinia*, where they are present in most vertebrae, with those along the caudal region extending laterally as far as the skin surface. In the posterior portion of the caudal region in that genus, the processes are as broad as the length of their vertebral centra, forming a nearly continuous horizontal bony shelf alongside the vertebral column. The structures are also well developed in aspredinids. The least developed condition is in *Parakysis*, where vestigial transverse processes are present only the posteriormost caudal vertebrae. In *Sisor*, most of the transverse processes are associated with the lateral bony plates formed from modified lateral-line ossicles (see character 111). The distal margin of each process contacts the mesial surface of its corresponding bony plate, sometimes forming a well-defined articulation.

73. Reduced number of pleural ribs (CI = 50, RI = 81).
    State 1 (five ribs): *Conta.*
    State 2 (three or four ribs): *Parakysis, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia,* [Aspredinidae = ?].

Siluriforms primitively have six or more pairs of fully formed pleural ribs. In the taxa above, there is an apomorphic reduction in the number of pleural ribs to five or fewer. The numbers are consistent enough to allow recognition of two states in this character, one of which (state 2) represents a more extreme reduction. *Conta* usually has five normal pairs of ribs and is the only taxon assigned state 1, although a sixth vestigial rib is present on one side of one specimen examined. The closest condition outside the assemblage above is found in *Sisor*, but here all six pairs are well developed, which distinguishes it from the variable condition observed in *Conta*. All other members of Sisori-

dae, Akysidae, and Amblycipitidae have seven or more pleural ribs. All aspredinids have state 2, except for *Xiliphius,* which shows the plesiomorphic condition; hence the uncertain coding for that taxon.

74. First two pleural ribs flattened and expanded (CI = 100).

Conta.

The pleural ribs in catfishes are primitively simple rods of bone, sometimes slightly flattened, elongated, and tapering only slightly from base to tip. The first rib is usually somewhat thicker than the remaining ones but retains the same overall morphology. In *Conta,* the first and second ribs are flat and expanded, and laminar for most of their length. The modification is evident in both ribs but is more marked in the first, which has an elongate leaf-like shape. The condition differs from that observed in *Pseudecheneis* (cf. character 70) because in that taxon the dorsal expansion is not part of a general flattening of the rib.

75. Parapophysis of first rib-bearing vertebra directed anteriorly (CI = 100).

Gagata.

The parapophyses of free vertebrae in most members of the ingroup and in catfishes in general are primitively directed ventrolaterally or posteroventrolaterally. Uniquely in *Gagata,* the direction of the parapophysis of the first rib-bearing vertebra (probably the seventh in this taxon) has a strong anterior component, and the main axis of the parapophysis is directed anteroventrolaterally (see Fig. 47).

Pectoral Fins and Girdle

76. First proximal radial an elongated cartilaginous rod (CI = 50, RI = 50).

Parakysis, Amblyceps, Liobagrus.

The first proximal radial in siluriforms is plesiomorphically a compact and roughly round cartilaginous structure, often with an anterior process that extends somewhat into the base of the pectoral spine. In the taxa above, the first proximal radial is modified into an elongate rod of even width and roughly rectangular profile (Fig. 31). A nearly iden-
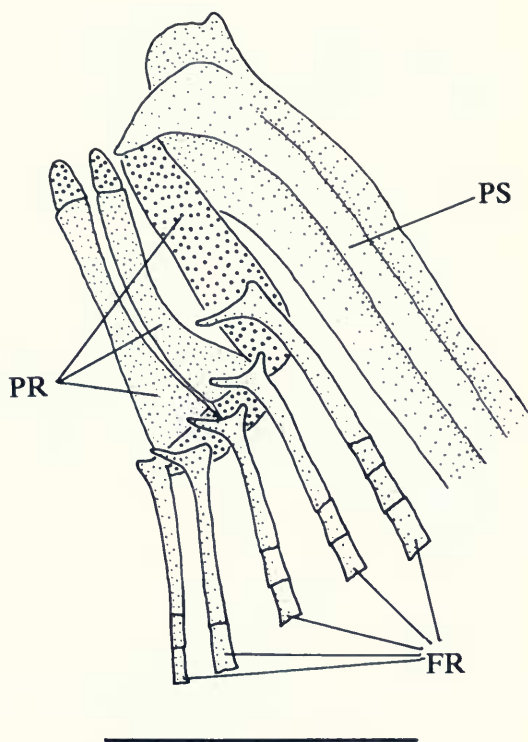

FIG. 31. *Parakysis anomalopteryx,* CAS 49421, pectoral fin ray support, ventral view. Larger stippling represents cartilage. Scale bar = 1 mm.

tical configuration of the first proximal radial is seen in Chacidae (Brown & Ferraris, 1988; pers. obs.), an occurrence postulated as homoplastic in view of the large number of nodes separating chacids from amblycipitids and *Parakysis* in siluriform phylogeny (de Pinna, 1993).

77. Anterior half of segments of pectoral fin spine elongate, almost parallel to axis of spine (CI = 33, RI = 50).

Acrochordonichthys, Akysis, Parakysis, Amblyceps, Liobagrus.

The peculiar structure of catfish pectoral spines has been studied in detail by Reed (1924a). In the plesiomorphic condition for the order, the various segments are disposed in an imbricated pattern that forms the shaft of the spine. Each of the segments that form the spine has roughly a short "V" morphology (Fig. 32A), with the two halves approximately the same size. The segmentation pattern is usually still evident in the fully ossified
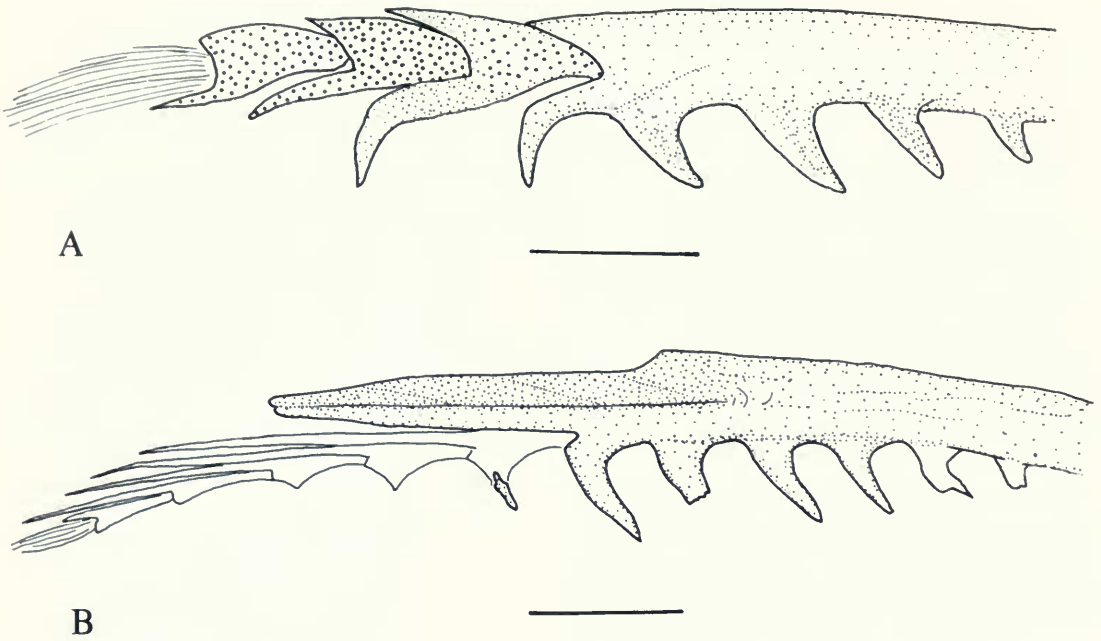
FIG. 32. Pectoral spines. **A,** *Glyptothorax pectinopterus,* BMNH 15445, left spine, ventral view (inverted). **B,** *Akysis* sp. 1, UMMZ 214907, left spine, dorsal view. First free segment in **A** partially ossified. Larger stippling represents unossified areas. Scale bars = 1 mm.

adult stage, and each segment extends only for a small portion of the total length of the spine. In the derived condition, the anterior half of each segment is elongated to such an extent that the actual pattern of formation of the spine becomes partly obscured (Fig. 32B). The long arms of adjacent segments are nearly parallel to each other and to the main axis of the spine. These modifications seem to be associated with an extremely fine tip of the spine in the fishes with the derived condition.

78. Proximal pectoral radials 2 and 3 flared at distal tip (CI = 100).

Glyptosternoids.

The ossified proximal pectoral radials in siluriforms primitively expand evenly and gently from base to tip. In glyptosternoids, these radials expand enormously near their distal end, assuming a flared morphology (Fig. 33). The greatly expanded distal end of the radials is apparently associated with the large number of pectoral fin rays

in those fishes (character 80), which are disposed in a round fan-like arrangement.

79. Coracoid with ventral process (CI = 33, RI = 75).

Bagarius, Conta, Erethistes, Erethistoides, Glyptothorax, Hara, Laguvia, [*Nangra* = ?], *Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

The coracoid in siluriforms primitively lacks major processes on its ventral surface. In the taxa above, there is a well-defined process extending directly posteriorly from the ventral surface of the bone (Fig. 34). The length of this process varies widely among taxa, ranging from shorter than the anteroposterior width of the cleithrum to long enough to reach or pass the anterior tip of the basipterygium. In some cases, the shaft of the process is extended anteriorly and ankyloses or fuses with the ventral surface of the cleithrum. Within *Nangra,* the process is absent in *N. nangra* and present, albeit small, in *N. viridescens,* a distribution that casts doubt on the precise coding of this character in the genus. In *Bagarius,* there is a

well-defined flange ventrally in the coracoid, in the position of and with an orientation corresponding to the basal portion of the process in other taxa. This flange is considered homologous to the process, representing either a very reduced or an incipient condition in its development. Mo and Chu (1986, p. 343) illustrated this process in some species of *Glyptothorax* that were not available for direct examination in this study.

Elsewhere within siluriforms, a cleithral process similar to that described above is present in scoloplacids (Bailey & Baskin, 1976, who also noted its presence in doradids; see also Schaefer, 1990), many if not all loricariids (Schaefer, 1987), doradoids, and probably also callichthyids (where the putative process is obscured by large bony expansions). In all cases, however, these outgroups have been shown to be part of larger assemblages whose other members lack the derived condition (cf. Schaefer & Lauder, 1986; Schaefer, 1987; de Pinna, 1993).

80. Eleven or more pectoral fin rays (CI = 100, RI = 100).

Glyptosternoids, *Pseudecheneis*.

There is a large variation in the number of pectoral fin rays in siluriforms. For the group under study, the plesiomorphic count of 8–10 rays seen in most catfish outgroups is also postulated here to be plesiomorphic. In *Pseudecheneis* and glyptosternoids, pectoral fin rays range from 11 (*Exostoma*) to 17 (*Pseudexostoma*).

81. Humeral process absent (CI = 50, RI = 50).

Parakysis, glyptosternoids, *Pseudecheneis*.

The humeral process of the pectoral girdle, a roughly triangular, pointed process directed posteriorly on the upper limb of the cleithrum, is present in the vast majority of catfishes. It is almost always present in the group under study, although in some taxa it is poorly developed, as in amblycipitids. The only ingroup taxa where the humeral process is completely absent are *Parakysis,* the glyptosternoids, and *Pseudecheneis*. In *Pseudecheneis,* a small splint of bone marking the attachment of the humerovertebral ligament (cf. character 64) may represent a remnant of the humeral process. If so, the character is still valid as evidence at the level of generality proposed because the condition in *Pseudecheneis* is still the
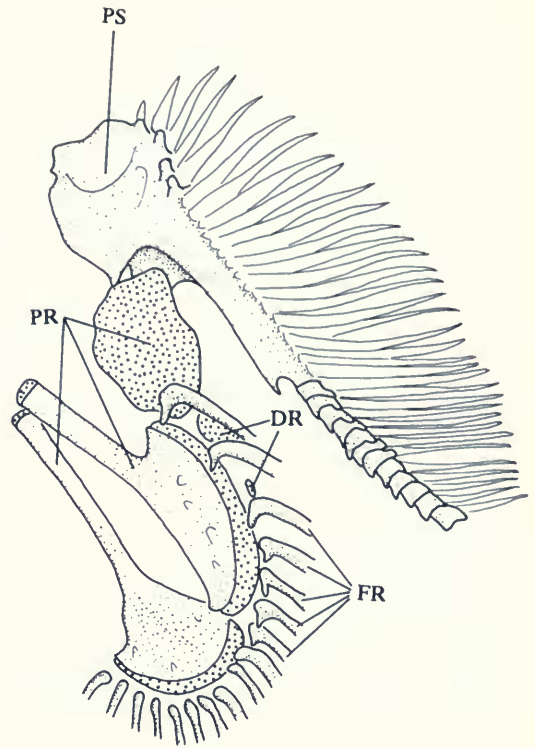
FIG. 33. *Pseudexostoma yunnanensis,* NRM 25124, left pectoral fin ray support, ventral view. Larger stippling represents cartilage. Scale bar = 1 mm.

most reduced in the ingroup other than that in glyptosternoids and *Parakysis*.

82. Upper limb of cleithrum with mesially directed laminar expansion (CI = 100, RI = 100).

Glyptosternoids, *Pseudecheneis*.

The plesiomorphic upper limb of the catfish cleithrum does not extend markedly toward the midline. The space between the two upper limbs of the cleithra are thus filled with unconstrained soft tissue. In glyptosternoids and *Pseudecheneis,* the upper limb has a large mesially directed laminar expansion, which in some cases (as in *Pseudexostoma*) forms almost a complete bony wall separating the head from the trunk regions, leaving only a narrow passage for the esophagus.

FIG. 34. *Conta conta*, UMMZ 208632, pectoral girdle, ventral view. Arrow indicates posterior process on coracoids. Scale bar = 1 mm.
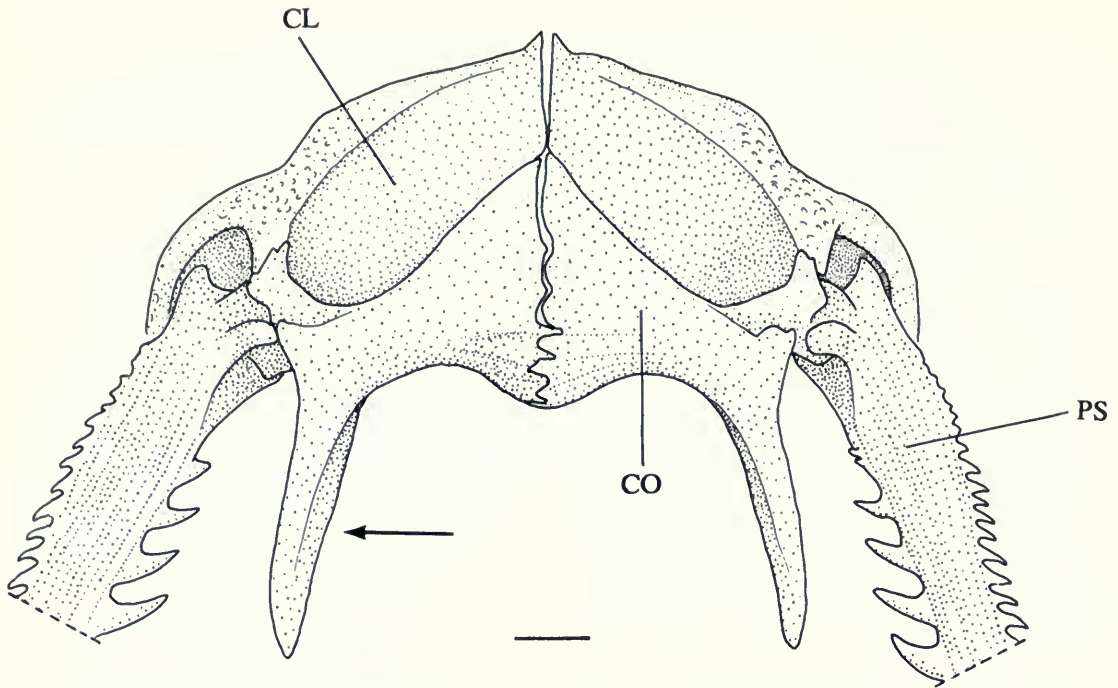
83. Anterior margin of pectoral fin spine with notch visible in dorsal view (CI = 100).

Akysis.

The fully developed pectoral fin spine in catfishes, despite its rather complex morphogenesis (Reed, 1924a), is primitively a cylinder of bone, roughly round or ovoid in cross-section. Although serial structures such as dentations or serrations are frequently present, there are no significant alterations of the shape of the shaft of the spine. As seen for character 87, some ingroup taxa have pouch-like depressions in the dorsal- and sometimes also in the pectoral fin spines. Uniquely in all *Akysis* species examined, the pectoral fin spine additionally has a well-defined notch located approximately at the midlength of its anterior margin (Fig. 32B). This notch is easily visible in dorsal aspect in cleared-and-stained preparations and is associated with the pouch-like modifications in the same spine of those fishes. A similar notch is sometimes also observed in the anterior margin of the dorsal fin spine, but there it is usually less well defined. The pectoral spine notch in *Akysis prashadi* was illustrated by Hora (1936, p. 201, Fig. 1).

84. Anterior margin of pectoral spine with serrations (CI = 50, RI = 83).

Conta, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia, Sisor, [Aspredinidae = ?].

The posterior margin of the pectoral spine in catfishes primitively has a series of pointed denticulations, usually slightly curved toward the base of the spine. The anterior margin of the spine, contrastingly, lacks such dentations in the primitive condition. In the derived condition, serrations similar to those along the posterior margin are also present along the anterior margin of the spine. In aspredinids, the derived condition is present in all species examined except for *Amaralia, Xyliphius,* and hoplomyzontins, hence the doubtful condition for Aspredinidae.

85. Internal support for pectoral fin rays small in size (CI = 50, RI = 75).

Conta, Erethistes, Erethistoides, Hara, Aspredinidae.

The internal support for pectoral fin rays in siluriforms, composed of distal and proximal radials, primitively forms a complex whose lateral (ray-bearing) surface is at least twice as long as the

diameter of the base of the pectoral spine. In the derived condition, the internal ray supports are small in overall size, their ray-bearing surface being shorter or only slightly longer than the basal diameter of the pectoral spine.

Dorsal Fin and Support

86. Extensive contact between anterior and posterior nuchal plate elements (CI = 100, RI = 100).

Conta, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia.

In many siluriforms, the first and second pterygiophores of the dorsal fin have dorsal expansions on the body surface. These expansions, which are often exposed on the surface of the skin, often appear as plates and indeed are referred to as nuchal plates. Primitively in catfishes, there are three nuchal plates: anterior, median, and posterior (Royero, 1987). In the ingroup in question, the primitive anterior and median plates are represented by a single ossification (it is still unclear whether this happens by fusion or loss of one of the elements), a trait the ingroup shares with a variety of other siluriforms. There is much variation of detail in the morphology of the nuchal plates, but when more than one is present their contact is narrower than the anteroposterior width of each individual plate. In the taxa above, the pterygiophore expansions are adpressed to one another along their common surface and the length of contact is larger than the anteroposterior width of each individual plate (Fig. 35).

87. Second dorsal fin spine with medial ridge along its anterior surface, forming bilateral longitudinal pouches (CI = 33, RI = 50).

Acrochordonichthys, Akysis, Parakysis, Amblyceps, Liobagrus.

The anterior surface of the catfish second dorsal fin spine is primitively a simple convex structure from base to tip. In the derived condition, the anterior surface of the spine has two deep lateral longitudinal grooves, which leave a medial anterior keel-like ridge between them. The soft tissues associated with the anterior surface of the spine form a pair of bilateral pouches along the grooves. The whole complex in these taxa may serve as storage for some substance associated with the dorsal spine. The integument around the spine in
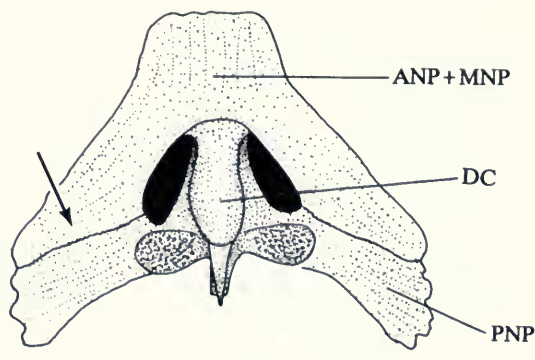

Fig. 35. *Hara hara*, UMMZ 208748, nuchal plates, dorsal view, dorsal fin spines removed. Arrow indicates contact between anterior and posterior nuchal plate elements. Scale bar = 1 mm.

some of the taxa above is easily retracted toward the base of the spine shaft, revealing an extremely sharp tip and in the process squeezing out whatever content is inside the pouches. This arrangement suggests the presence of a toxic substance associated with function of the dorsal spine as a defense mechanism.

The presence of gland cells associated with the dorsal and pectoral spines in some siluriforms has been well documented by Reed (1924b, pp. 257–258), who stated that

> the spines [in catfishes] are covered with integument, so that when inflicting a wound it is necessary for the spine to first puncture the skin which covers it. In addition to the skin wound thus produced, the growing end of the spine is multilated [sic], since the developing caps are soft and not firmly attached to the next older cap.

Reed (1924b, p. 257) contrasted this condition with that seen in other teleosts with poisonous secretions associated with fin spines where

> the spines are naked in the distal portion, and are so related to the gland and surrounding integument that there is formed a mobile sheet, which easily slips away from the apex of the spine, and at the same time forms a reservoir in which secretion may be stored against later needs.

The derived condition observed for the taxa above is intermediate between the two conditions described by Reed. The skin covering the spine is retractable and forms a reservoir, but it is obviously punctured by the spine in action, which also loses its soft tip in the process. A detailed histo-
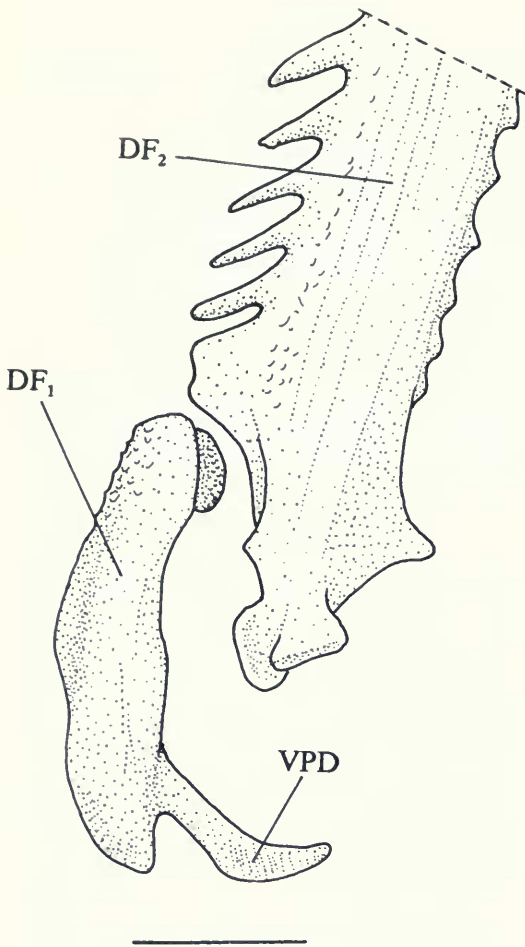
FIG. 36. *Conta conta,* UMMZ 208632, dorsal fin spines, lateral view. Scale bar = 1 mm.

logical study of the dorsal fin spine in akysids and amblycipitids is necessary to understand the function of the structure in those taxa.

88. Ventral arms of first dorsal fin spine with posterior processes attached dorsal to their tip (CI = 100, RI = 100).

Bagarius, Conta, Erethistes, Erethistoides, Gagata, [glyptosternoids = ?], *Glyptothorax, Hara, Laguvia, Nangra,* [*Pseudecheneis* = ?], *Pseudolaguvia,* [*Sisor* = ?], [Aspredinidae = ?].

The first dorsal fin spine in catfishes is proximally divided into two broad arms not particularly elongate ventroposteriorly. The ventral tips of each of these arms are sometimes extended posteroven-

trally in the form of a long process continuous with the arms themselves, as in amblycipitids, most akysids, and many doradoids. In the derived condition for the taxa above, the process of each arm is inserted not at its tip but rather at a point dorsal to it (Fig. 36). This insertion site makes the whole arm of the spine appear bifurcated, with one side of the bifurcation continuous with the rest of the spine and the other diverging posteroventrally from it. The taxa with this character coded as missing are those in which the whole first spine is absent or extremely reduced (aspredinids, glyptosternoids, *Sisor*) or in which the spine is present but lacks ventral processes (*Pseudecheneis*).

89. Element corresponding to second dorsal fin spine not spinous (CI = 100, RI = 100).

Glyptosternoids, *Pseudecheneis.*

The second dorsal fin spine in catfishes (often referred to as the dorsal spine) is primitively modified into a pungent structure, with a morphology unique for the group (Reed, 1924a). A typical second spine is present in nearly all members of the group studied, with the exception of *Pseudecheneis* and the glyptosternoids. Those two exceptions are clearly derived within siluriforms. Even in other members of the ingroup with a nonpungent spine, such as *Sisor,* the morphology of the ray retains the condition primitive for catfishes, with a series of imbricated V-shaped segments formed by successive branchings of one half-ray. Only in the two taxa above is the ray completely nonspinous, composed of simple rectangular lepidotrichia (except for the processes for the pinnate expansions of the dorsal fin in some glyptosternoids) similar to those seen in more posterior dorsal fin rays.

90. Posterior nuchal plate with anterior process forming facet for articulation with anterior nuchal plate (CI = 100, RI = 100).

Acrochordonichthys, Akysis, Breitensteinia, Parakysis, Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids, *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor,* Aspredinidae.

Primitively in siluriforms, the anterior and posterior nuchal plates, when they contact each other, lack facet-like bony structures at the area of contact. In amblycipitids, the distal margin of the posterior plate is twisted dorsally to meet its counterpart anteriorly and may be somewhat thickened

at this site. However, it lacks a well-differentiated process. In the apomorphic state, the posterior nuchal plate has a well-defined strut of bone forming a facet that articulates anteriorly with the anterior nuchal plate element. This process is well differentiated and is not simply an enlargement of the distal margin of the plate. It is located proximally relative to the lateral margin of the plate. The anterior and posterior nuchal plates are very reduced in glyptosternoids and do not contact each other. Often, the pterygiophore portion corresponding to the first nuchal plate is altogether absent in that taxon. However, when both plates are present, they are linked by a ligament that occupies the same position as a bony bridge in other taxa. There is a bony protuberance on the anterior margin of the posterior nuchal plate at the site where the ligament attaches. This protuberance is postulated as homologous to the process seen in the remaining terminal taxa with the derived condition, therefore serving as evidence that glyptosternoids display the apomorphic state for this character. The extensive surface of contact between the first and second nuchal plates in aspredinids and all taxa referred to below in the family Erethistiidae modifies the process such that it is wider than long. The facet-like structure of the contact is still evident, however, on the mesial portion of the posterior plate. The anterior and posterior nuchal plates are distally fused to each other in adult specimens of *Parakysis verrucosa* examined in the area of interest for this character, which makes it uncertain whether or not the process is primitively present in this taxon. Nevertheless, this fusion has apparently not yet taken place in the much smaller examples of *P. anomalopteryx* available; these clearly show an anterior process on the posterior nuchal plate (Fig. 37). The process at this stage is linked to the anterior nuchal plate by a ligament in an arrangement similar to that described above for some glyptosternoids. On the basis of this data, *Parakysis* is also assigned the derived condition for this character. Examination of a more complete ontogenetic series will be necessary to confirm the coding of this character for both *Parakysis* and glyptosternoids.

91. Ventral tip of first dorsal fin pterygiophore and corresponding neural spines with contacting facets (CI = 100, RI = 100).

Acrochordonichthys, Akysis, Breitensteinia, Parakysis, Amblyceps, Liobagrus, Bagarius, Conta, Erethistes, Erethistoides, Gagata, glyptosternoids,
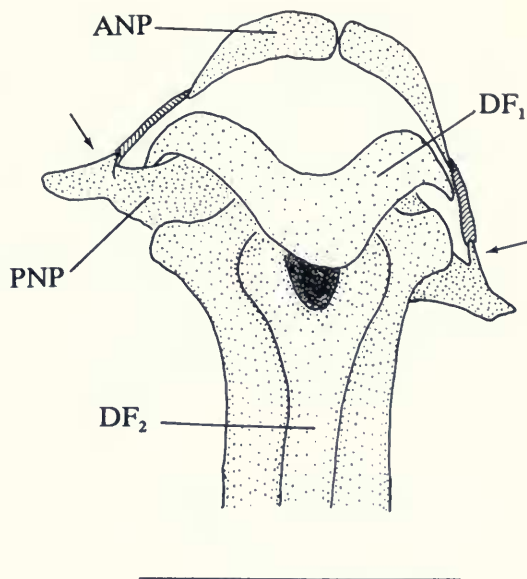

FIG. 37. *Parakysis anomalopteryx,* CAS 49421, putatively juvenile condition of dorsal fin spines and nuchal plates, dorsal view. Arrows indicate anterior processes on posterior nuchal plates. Wavy lines represent ligaments. Scale bar = 1 mm.

Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia, Sisor, Aspredinidae.

The first dorsal fin pterygiophore in siluriforms usually extends ventrally to fit between the arms of the bifurcated neural spine of the complex centrum (Royero, 1987). Primitively within the order, both the ventral portion of the pterygiophore and its corresponding neural spine are formed mostly of smooth laminar bone, frequently with long laminar flanges for muscle insertion. In all terminal taxa treated in this study, the ventral portion of the first pterygiophore and the distal tip of the neural spine of the complex centrum are composed of thick, rugose nonlaminar bone. Additionally, the surfaces of both structures are expanded at their region of contact, forming a facet-like thickening on the lateral face of the pterygiophore. The rugose aspect is more pronounced where the surfaces are in contact, i.e., the lateral surface of the pterygiophore and the mesial surface of the distal tip of the neural spine. All these characteristics seem to represent an incipient stage of the modifications that lead to the formation of a stridulatory apparatus, described below as a character of a more restrictive clade (cf. character 109).
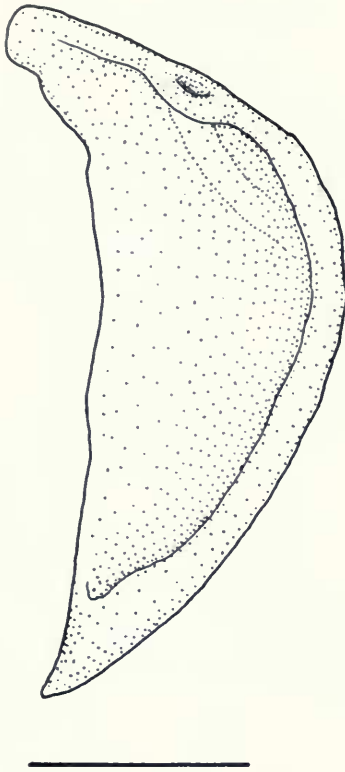
FIG. 38. *Erethistes pusillus*, UMMZ 208697, right lacrimal, dorsal view, anterior on top. Scale bar = 1 mm.

92. Posterior nuchal plate straight and thin, its width approximately even from base to tip (CI = 100, RI = 100).

[*Bagarius* = ?], *Gagata, Nangra*.

The plesiomorphic condition for the posterior nuchal plate in siluriforms is that of a wide plate of bone, approximately twice as long as broad and expanding gently from base to tip. Its margins are usually curved, forming a convex profile. In *Gagata* and *Nangra*, the posterior nuchal plate is different from that primitive condition in several respects. It is roughly five times as long as broad, its width either narrows or remains constant from base to tip, and its margins are straight in dorsal view. The character is variable in *Bagarius*, with the plesiomorphic condition seen in small *B. bagarius* (UMMZ 186793) and the apomorphic state clearly present in the largest *B. yarrelli* available for study (LACM 38294-55). Medium-sized *B. yarrelli* show a condition intermediate between the derived and primitive states, which seems to in-

dicate that the apomorphic state may only become evident in large specimens of the genus. However, in the absence of any ontogenetic information on species other than *B. yarrelli,* this character is coded as missing for *Bagarius*.

Laterosensory System

93. First lateral-line ossicle enlarged, adjoined to posterior portion of supracleithrum (CI = 50, RI = 75).

Acrochordonichthys, Akysis, Breitensteinia, Parakysis, Aspredinidae.

The lateral-line sensory canal in siluriforms is usually enveloped by a series of tubular ossicles, believed to be the only remnants of scales in the fishes of this order (Fink & Fink, 1981). In the plesiomorphic condition, the first (anteriormost) ossicle is similar to those following and is loosely connected with the portion of the supracleithrum where the lateral-line canal emerges from the skull. The lateral-line canal, therefore, runs exclusively through soft tissue for a distance between the back of the skull and the first ossicle. In the taxa above, the first ossicle is more heavily ossified than the subsequent ones and is also larger and more complex in shape. Additionally, it is closely adjoined to the back of the skull (Fig. 10). The lateral-line canal emerges from the supracleithrum and goes directly into the first ossicle, being thus almost continuously enclosed in bone until the posterior end of the first ossicle. Within *Akysis* species, the character is fully developed only in *Akysis* sp. 1, which includes the largest specimens of the genus available for study. In remaining *Akysis* species, the derived condition is not as clearly present, perhaps as a result of the juvenile condition of these small specimens. The first lateral-line ossicle, however, is clearly larger than those remaining and is more closely associated with the posterior portion of the neurocranium than it is in the plesiomorphic condition.

94. Lacrimal modified into a bowl-shaped structure located ventrolaterally to nasal capsule (CI = 50, RI = 86).

Conta, Erethistes, Erethistoides, glyptosternoids, Hara, Laguvia, Pseudecheneis, Pseudolaguvia.

The lacrimal (= first infraorbital) in catfishes displays a large amount of morphological varia-

tion not yet interpreted in a phylogenetic context. Usually it is composed of a tubular portion that encloses the anterior part of the infraorbital laterosensory canal, a plate-like portion developed to different degrees among various taxa, and one or more processes in various positions. Although it is futile to attempt to describe what would be the generalized primitive condition of the whole lacrimal for siluriforms, some unique conditions can confidently by hypothesized as apomorphic. The condition in the taxa above is one of them. In those taxa, the lacrimal is modified into a large and simple bowl-like structure, adpressed to the ventrolateral surface of the nasal capsule and apparently providing partial shielding for it (Fig. 38). The canal portion normally associated with the lacrimal is still present and extends along the dorsal portion of the bowl without interrupting its smooth profile.

95. Nasal with expansions beyond canal-bearing portion (CI = 100).

Akysis.

The nasal in catfishes is primitively a simple tubule lining a corresponding portion of the laterosensory canal system. It normally lacks any significant expansions of bone beyond the canal-bearing tube. In all *Akysis* species examined, the nasal has shelf-like expansions on its dorsal surface, extending considerably beyond the canal-bearing tube along its whole length (Fig. 39). The nasal in *Acrochordonichthys* is considerably thickened compared with the plesiomorphic condition in catfishes. Despite the heavy ossification, however, the extent of ossification beyond the canal-bearing portion is minimal in that genus and very different from the condition observed in *Akysis*.

96. Nasal elongated anteriorly to the level of anterior margin of mesethmoid cornua (CI = 33, RI = 0).

Bagarius, Nangra, Aspredinidae.

The nasal bone in catfishes primitively does not extend anteriorly to the anterior margin of the mesethmoid cornua. In aspredinids, *Bagarius,* and *Nangra,* the nasal is elongated, and its anterior tip reaches or passes the anterior margin of the underlying mesethmoid cornua.
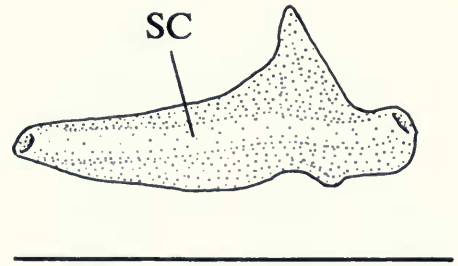

FIG. 39. *Akysis leucorhynchus,* USNM 109636, left nasal, dorsal view, anterior to right. Scale bar = 1 mm.

97. Anterior portion of lateral line running closely in parallel to lateral margin of Weberian lamina (CI = 100, RI = 100).

Conta, Erethistes, Erethistoides, Hara, Laguvia, Pseudolaguvia, Aspredinidae.

The lateral-line sensory canal and associated ossicles in catfishes primitively follow a path along the body of the fish without any close associations with internal skeletal structures. In the derived condition, the anterior portion of the canal follows closely the ventral rim of the lateral margin of the Weberian lamina (Figs. 11, 25). In cases where the lamina is curved, the canal follows the curve of the lamina.

98. Path of infraorbital laterosensory canal straight (CI = 50, RI = 50).

Acrochordonichthys, Akysis, Breitensteinia.

The infraorbital branch of the laterosensory system of the head in catfishes primitively follows a curved path roughly circling the ventral profile of the orbit (Arratia & Huaquin, 1995). In the taxa above, the infraorbital canal is straight or nearly so from the sphenotic to the lacrimal (Fig. 10).

99. Lacrimal with dorsal mesially directed shelf-like portion (CI = 50, RI = 75).

Acrochordonichthys, Akysis, Breitensteinia, Parakysis, Aspredinidae.

The lacrimal (first infraorbital) in siluriforms displays a large amount of morphological varia-
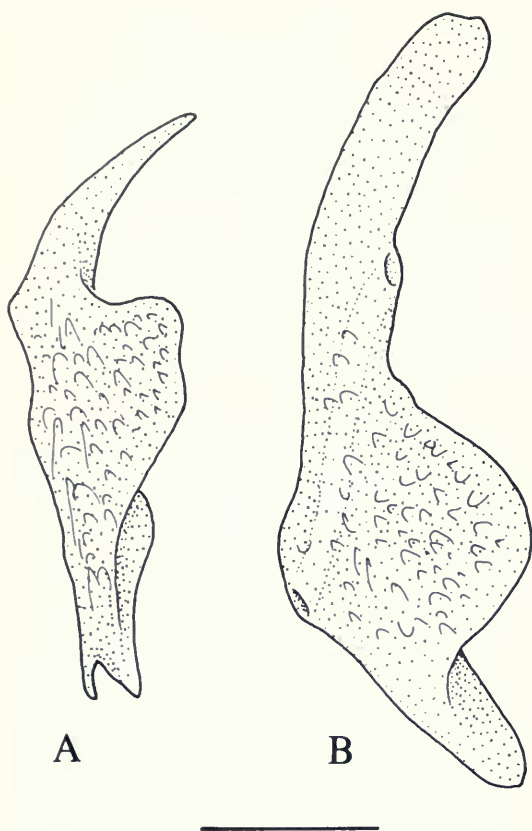
FIG. 40. Left lacrimals in dorsal view, anterior on top. **A**, *Dysichthys* sp., AMNH uncat. **B**, *Acrochordonichthys rugosus*, ZRC 4415. Scale bar = 1 mm.
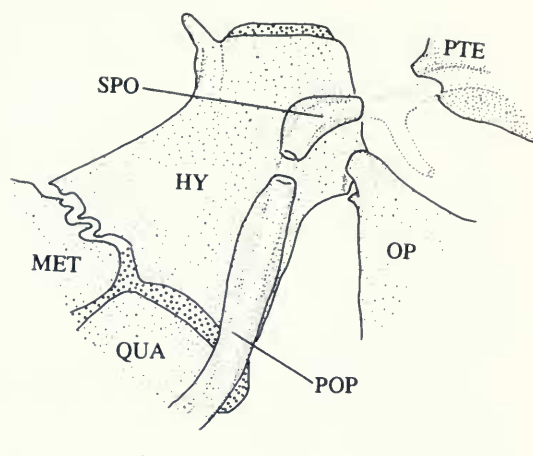

FIG. 41. *Nangra nangra*, CMK 6369, dorsal portion of preopercular branch of laterosensory canal system and related structures. Larger stippling represents cartilage. Scale bar = 1 mm.

tion, which makes it difficult to hypothesize its general plesiomorphic morphology (see discussion of character 94). Rather, it seems that the only way to adequately describe the phylogenetically informative variation in that bone is to subdivide it into various individual characters representing subsets of its general morphology. The character described here relates to the dorsal margin of the lacrimal, an area that in most catfishes is flat and devoid of marked modifications of shape. In the taxa above, the dorsal surface of the lacrimal has a large curved expansion extending dorsomesially (Fig. 40). The expansion is thick, not laminar, and usually has ornamentations on its surface.

100. Nasal adpressed to margin of neurocranium for posterior two thirds or more of its length,

anterior portion abruptly diverging laterally (CI = 100, RI = 100).

Erethistes, Erethistoides, Hara.

The nasal in catfishes is primitively located along the lateral margin of the mesethmoid but separated from it throughout its length by a space greater than the width of the nasal. In the derived condition, the posterior half or more of the nasal's length is adpressed to the lateral margin of the mesethmoid, and its anterior portion abruptly diverges laterally.

101. Dorsal half of suprapreopercle strongly curved posteriorly, making nearly 90° angle with ventral half of bone (CI = 100, RI = 100).

Gagata, [Glyptothorax = ?], Nangra.

The suprapreopercle, a common ossification in the ingroup under study and many other catfishes, is a tubular ossicle lining the branch of the sensory canal system between the dorsal tip of the preopercle and the pterotic. Primitively in the order, the suprapreopercle is a roughly straight tube, frequently inclined posteriorly relative to the dorsal tip of the preopercle. In the derived state, the dorsal half of the suprapreopercle is strongly curved posteriorly, forming an almost 90° angle with its ventral half (Fig. 41).

Within *Glyptothorax*, there is widespread variation in the states of this character, not only among

the various species but also on occasion between different specimens of the same species, and sometimes even between the right and left sides of the same individual. This variation cannot be adequately treated in this study, and this character is coded as missing for *Glyptothorax.*

102. Hyomandibula with bony tunnel enclosing branch of the laterosensory canal between preopercle and pterotic (CI = 100).

Aspredinidae.

As described for character 101, the branch of the laterosensory canal system between the preopercle and the pterotic is typically enclosed in an independent ossification called the suprapreopercle. In aspredinids, that canal branch is instead enclosed in a bony tunnel in the hyomandibula. This tunnel probably represents a suprapreopercle indistinguishably fused to the hyomandibula, because the hyomandibula is primitively not a canal-bearing bone. Nonetheless, there is no sign of an independent suprapreopercle in even the youngest specimen of the family examined (a representative of *Aspredo aspredo,* USNM 226072) or in the possibly paedomorphic hoplomyzontins.

Pelvic Fins and Girdle

103. Basipterygium with ventral longitudinal keel, extending anteriorly alongside internal arm (CI = 50, RI = 85).

Bagarius, Conta, Erethistes, Erethistoides, Gagata, [glyptosternoids = ?], *Glyptothorax, Hara, Laguvia, Nangra, Pseudecheneis, Pseudolaguvia,* [*Sisor* = ?].

The ventral surface of the basipterygium in catfishes is primitively flat, without prominent processes or flanges. In the taxa above, there is a conspicuous laminar flange on the ventral surface of the basipterygium. It usually originates on the main portion of the bone and extends anteriorly alongside the ventral surface of its internal arm (Fig. 42). For most of its length, the structure is a low flange, but in the majority of taxa there is a well-defined, small portion where it is abruptly more prominent. The process is reduced but still present in *Bagarius, Pseudecheneis, Erethistes, Erethistoides,* and *Hara.* Among glyptosternoids exam-
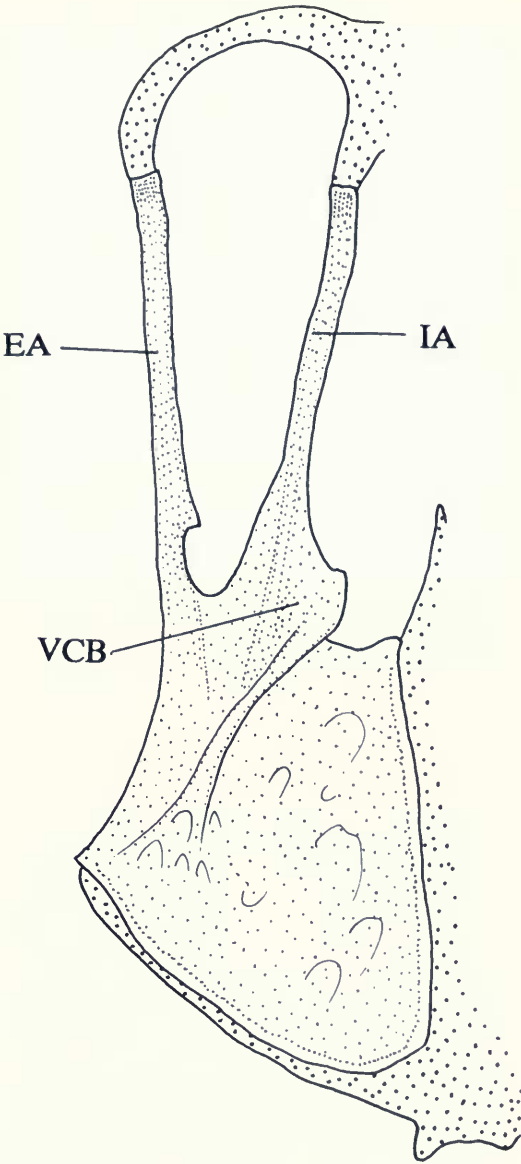

FIG. 42.   *Laguvia ribeiroi,* UMMZ 208955, right basipterygium, ventral view. Larger stippling represents cartilage. Scale bar = 1 mm.

ined, only *Exostoma labiatum* has the derived state and in a rather reduced condition (Fig. 43). Therefore, this character was coded as missing for glyptosternoids.
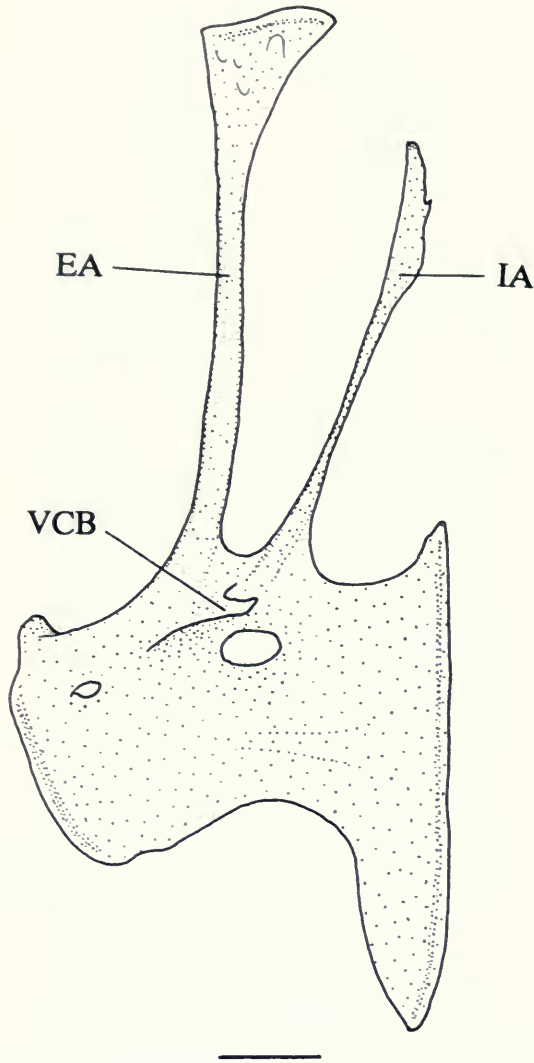
FIG. 43. *Exostoma labiatum*, NRM 25105, right basipterygium, ventral view. Scale bar = 1 mm.

taxa, as in amphiliids, it is located on the dorsal surface of the basipterygium.

104. External arm of basipterygium abruptly expanded distally (CI = 100).

Glyptosternoids.

In the primitive condition, the anterior arms of the basipterygium in siluriforms expand only slightly or instead narrow from base to tip. In cases where they expand, the expansion proceeds along their whole length. In all glyptosternoids, the narrow external arm of the bone is abruptly expanded near its anterior tip (Fig. 43). The internal arm retains the primitive morphology.

105. Posterior cartilage of basipterygium ramified (CI = 100).

Bagarius.

The posterior cartilage of the basipterygium in siluriforms is primitively a relatively short structure bordering a more or less extensive part of the posterior process of the bone (Shelden, 1937). In *Bagarius,* this cartilage is markedly elongated posteriorly and distally ramified into a short dendritic arrangement. A somewhat similar condition is seen in the subfamily Cetopsinae of the Cetopsidae (de Pinna & Vari, 1995). In the Cetopsinae, nonetheless, the dendritic portion of the cartilage is far longer than that observed in *Bagarius.* This difference, plus the fact that cetopsines and *Bagarius* are very distantly related in catfish phylogeny (de Pinna, 1993), indicates that the two conditions are not homologous.

106. Cartilage on posterior process of basipterygium reduced or absent (CI = 100).

Aspredinidae.

The posterior process of the basipterygium in siluriforms is usually lined mesially and posteriorly with a narrow but relatively extensive cartilage, often continuous mesially with the interbasipterygial cartilage. In the Aspredinidae, the cartilage either is reduced to a small distal plug isolated from the interbasipterygial cartilage (in aspredinines and bunocephalins) or is totally absent (in hoplomyzontins).

The flange is an attachment point for the protractor ischii muscle, which pulls the pelvic girdle anteriorly when contracted (Saxena & Chandy, 1966). Elsewhere within siluriforms, a very similar structure is present in Amphiliidae (Skelton, 1985, pp. 275, 276, 287). However, here the flange is on the dorsal surface of the bone instead of the ventral, therefore indicating nonhomology. A somewhat similar keel is present in callichthyids (Reis, 1993) and hoplomyzontin aspredinids, but in these

107. Anterior arms of basipterygium undifferentiated from main part of bone (CI = 100).

Aspredinidae.

In nearly all siluriforms the basipterygium has two anterior arms with cartilages at their tips (Shelden, 1937). Uniquely in aspredinids, there is no differentiation between the body of the basipterygium and its arms, and the whole pelvic skeleton is represented by a single plate. Anterolaterally along the edge of the bone, a single cartilage extends from the region of fin-ray attachment to the anterior end of the basipterygium. Anterior basipterygial arms are also undifferentiated in scoloplacids (Schaefer, 1990, pp. 196–197). However, these arms are present in remaining loricarioids, indicating that the condition in that family is autapomorphic.

Miscellaneous

108. Epural curved (CI = 100).

Parakysis.

The epural in catfishes, when present, is primitively a straight or nearly straight rod of bone in lateral view (cf. Lundberg & Baskin, 1969). In *Parakysis,* the bone is markedly curved posteriorly, leaving an elliptical space between it and the uroneural.

109. Stridulatory apparatus (CI = 66, RI = 80).
State 1: *Conta.*
State 2: *Gagata, Nangra, Sisor.*

The presence of a stridulatory apparatus is among the most interesting morphological modifications seen in the ingroup under study. Although sound-producing adaptations are common and have long been known in siluriforms (see Geoffroy St. Hilaire, 1829; Tavolga, 1962, 1971, 1977), the specific mechanism seen in *Conta, Sisor, Nangra,* and *Gagata* is unique within the order. In these genera, the apparatus is formed by a modified contact between the neural spine of the complex centrum and the first dorsal fin pterygiophore (actually formed as a ventral extension of the supraneural that forms the anterior nuchal plate). The close connection between the two structures in itself is plesiomorphic for catfishes. In the derived state, however, the surfaces of contact are markedly en-

Fig. 44. *Gagata gagata,* AMNH 8358, SEM photograph, hemal spines of complex centrum, anterolateral view. Scale bar = 1 mm.

larged and mobile. Additionally, their surfaces of contact are crenulated, i.e., provided with a series of short parallel ridges on the lateral surface of the pterygiophore and on the mesial surface of the parapophysis (Figs. 44–47). These and other modifications form a well-differentiated stridulatory apparatus. The sound is produced when the ridged surface on the ventral tip of the supraneural and its counterpart on the neural arch rub against one another, and it can be simulated by manipulating the head of preserved specimens (as reported by Haddon, 1881). Two major versions of the apparatus exist. In one of them, coded as state 1 and seen only in *Conta,* the ventral ridged processes of the pterygiophore are separate and each has its own ridged area that contacts the neural spine arm on its side (Fig. 46). Sound-producing contact can be both on the right and left sides at the same time. In the other version, coded as state 2 and seen in the other three genera, the ridged surfaces of the pterygiophore are fused into a single median process, forming a round bony swelling with vertical ridges on its surface (Fig. 47). In this second version, the sound-producing contact can take place on the right or left sides of the modified neural
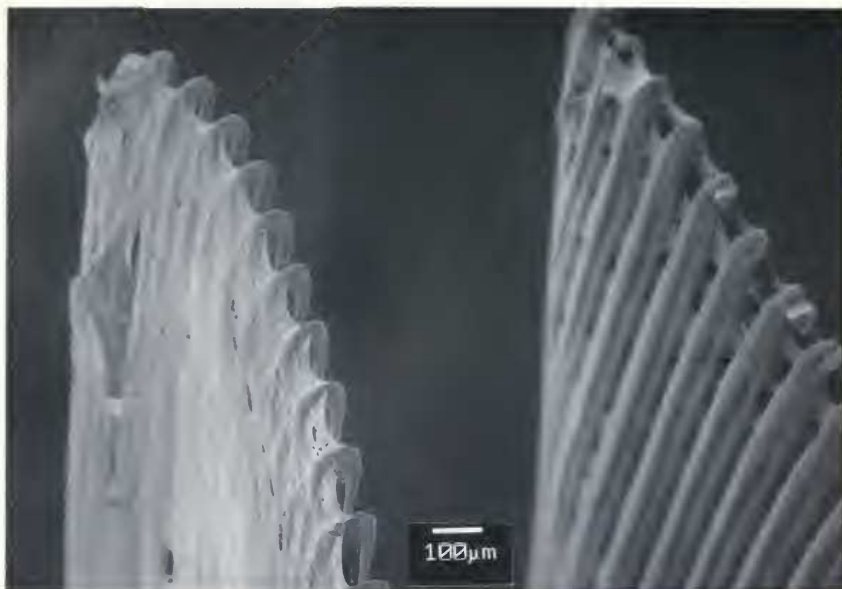
FIG. 45. *Gagata gagata*, AMNH 8358, SEM photograph, distal portion of hemal spines of complex centrum, showing internal ridges of stridulatory apparatus. Scale bar = 1 mm.

spine but not on both simultaneously. States 1 and 2 are ordered in this way because the ventral arms of the supraneural are primitively separate, and their fusion is therefore a subsequent step. The stridulatory apparatus in *Gagata* was described by Haddon (1881), and that of *Sisor* was described by Mahajan (1963). The apparatus is well developed and in accordance with state 2 in *Nangra viridescens,* but in *N. nangra* it seems to be somewhat atrophied and corresponds to state 1. *Nangra,* therefore, shows some ambiguity with regard to this character's coding. Despite that, the character is assigned state 2 instead of a missing code for this genus. The reason for this decision is that a missing code would imply, for parsimony calculations, that this character in *Nangra* could be assigned any of states 0, 1, or 2. However, the genus never lacks the stridulatory apparatus and consequently the character state can only be 1 or 2. Adequate treatment of this case will depend on methodological developments regarding treatment of missing codes for multistate characters in parsimony analysis.

110. Integument of thorax or thorax and abdomen modified into adhesive apparatus formed by patches of unculi underlain by ridges of integument (CI = 40, RI = 25).

State 1 (ridges oblique or parallel to body): *Conta, Glyptothorax, Laguvia, Pseudolaguvia.*

State 2 (ridges transverse to body): *Pseudecheneis.*

There is an extensive literature dealing with the morphology and evolutionary significance of the hill-stream adaptations in sisorids (e.g., Hora, 1922, 1923, 1930; Bhatia, 1950; Lal et al., 1966; Saxena & Chandy, 1966; Tilak, 1976). Among the most conspicuous of these specializations is the presence of an adhesive apparatus on the ventral surface of the body. The structure is formed by integumentary folds forming a pattern of ridges and grooves usually disposed in a roughly bilateral arrangement. The area covered by the ridges varies from a small arc immediately posterior to the branchiostegal membranes (as in some *Glyptothorax*; cf. Jayaram, 1981, pp. 255–259) to nearly the whole thoracic and abdominal region (as in *Conta*). Covering the integument ridges are patches of numerous unculi (cf. Fig. 48), which are projections of single epidermal cells of ostariophysans (Roberts, 1982; Arratia & Huaquin, 1995) and seem to play a major role in adhesion. Although densely distributed over the ridges, unculi are absent in the grooves of the adhesive apparatus (first
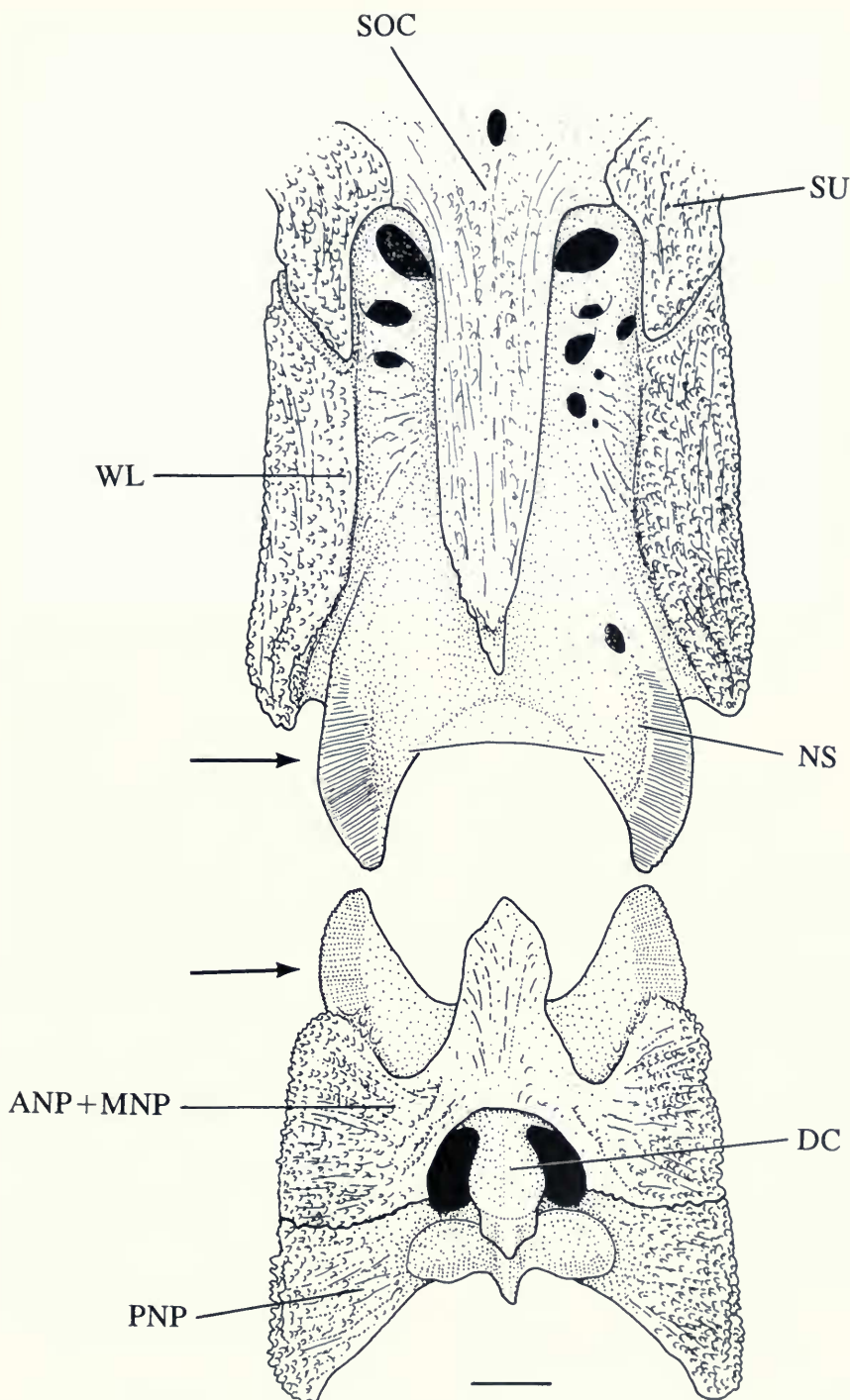
Fig. 46. *Conta conta,* UMMZ 208632, posterior portion of neurocranium and Weberian complex (above) and dorsal fin support (below, spines removed), dorsal view. Arrows indicate ridges of stridulatory apparatus; those indicated by lower arrow are seen by transparency. Upper and lower portions shown separated for clarity; their natural relative portion corresponds to an overlapping of the two arrows. Scale bar = 1 mm.
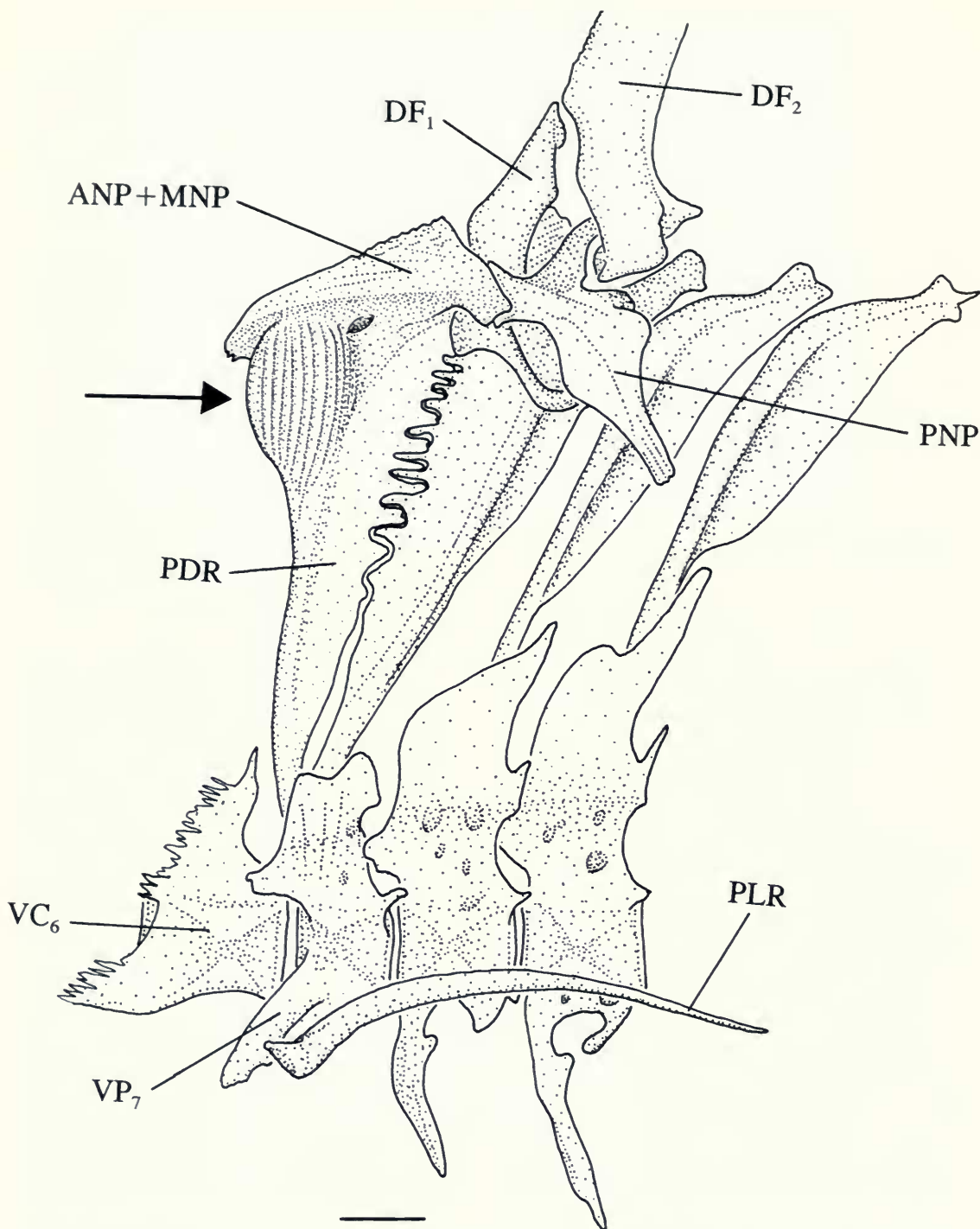
FIG. 47. *Gagata gagata,* AMNH 8358, dorsal fin support and associated vertebral elements, lateral view. Arrow indicates ridged sphere that forms part of stridulatory apparatus. This structure is located between the ridged surfaces of the neural spines shown in Figures 44 and 45. Scale bar = 1 mm.
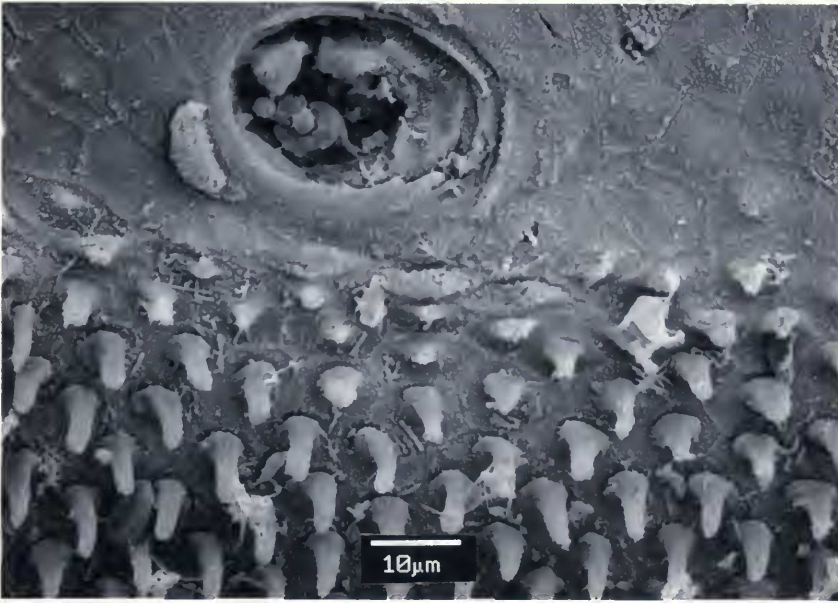
Fɪɢ. 48. *Pseudecheneis sulcatus,* ʙᴍɴʜ 1985.9.16:50, SEM photograph of adhesive apparatus. Notice profile of individual epithelial cells.

observed by Hora, 1922) (Fig. 49). There is a large degree of morphological variation in the adhesive apparatus among various taxa. The most deviant condition is found in *Pseudecheneis,* where the skin ridges are thick, flat, and oriented transversely relative to the longitudinal axis of the body (Fig. 49). However, the condition of the adhesive apparatus in juveniles of that genus is similar to that in other taxa. The integumentary folds in young *Pseudecheneis sulcatus* are oblique and gradually assume a transverse orientation with growth (Tilak, 1976). This observation not only corroborates that the adhesive apparatus in *Pseudecheneis* is homologous to that in other taxa but also indicates that transverse folds are derived relative to their oblique orientation. Therefore, this character is separated into two states, ordered accordingly. In state 1, the ridges of the adhesive apparatus are oblique or parallel to the longitudinal axis of the body, and in state 2, the ridges have a transverse orientation.

The presence of unculi, taken by itself, is plesiomorphic, because they are probably primitively present in most ostariophysans (Roberts, 1982) (however, they are absent in diplomystids; see Arratia & Huaquin, 1995). Also, the association of unculi with adhesive functions is not exclusive to sisoroids; it also occurs in the pectoral fin of am-

philiids (Roberts, 1982), seemingly with a similar function. What defines the derived condition discussed here is specifically the presence of well-defined unculi patches associated with prominent skin ridges on the thorax and/or abdomen. The whole structure is evident on the ventral aspect of the fish and normally visible with the naked eye. The fine structure of the adhesive apparatus in sisorids has been reported in a number of papers, summarized and added to by Roberts (1982). More recently, additional SEM observations on *Pseudecheneis* were reported by Singh and Agarwal (1991). For this study, SEM examinations corroborated observations previously made for that genus (Figs. 48, 49). Additionally, the SEM structure of the apparatus in *Conta* and *Laguvia* was examined for the first time (Figs. 50, 51) and was found to conform to the general morphology so far known for the thoracic adhesive apparatus in other taxa.

The first in-depth account of the adhesive apparatus in sisorids was by Hora (1922). According to that author, each of the unculi-bearing epidermal cells (then not referred to by this name) has a cell nucleus right at the base of the unculus; sometimes half of the nucleus is actually inside the unculus. This positioning probably indicates intense nuclear synthesis directed toward the un-
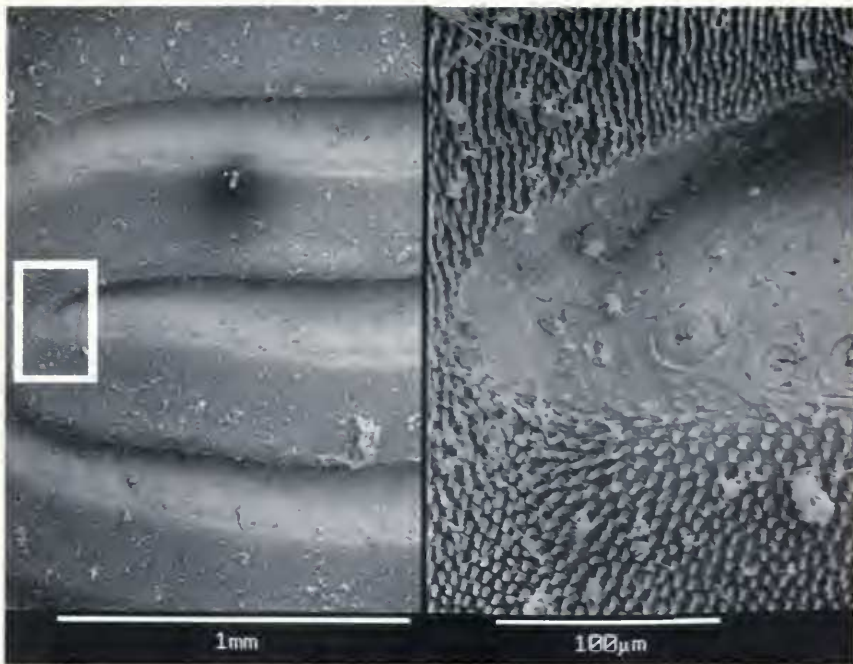
Fig. 49. *Pseudecheneis sulcatus,* BMNH 1985.9.16:50, SEM photograph of adhesive apparatus, showing transverse folds and limit between ridge (with unculi) and groove (naked) areas. At right is an enlargement of area framed by rectangle at left.

culus region. The cell nuclei are located deeper in the body of those epidermal cells that lack unculi, i.e., those lining the grooves of the adhesive apparatus (Hora, 1922). The taxonomic generality of these observations about the position of the nucleus remains to be determined.

111. Bony plates on surface of body (CI = 100).

Sisor.

The primitive catfish condition is the lack of bony plates on the surface of the body, as seen in diplomystids, cetopsids, pimelodis, bagrids, and all other basal or generalized siluriforms. An armored condition is certainly derived within the order, but the definition of a bony plate is rather loose, and their structural basis can be highly variable. Sometimes in the same taxon, plate-like structures are formed from widely different anatomical bases. In *Sisor,* the body is covered by three series of bony plates, each having a different structural basis. The series along the lateral sides of the body are formed by expanded lateral-line ossicles, which posteriorly become closely associated with the distal margin of the vertebral transverse processes (see character 72). Meanwhile, the

series along the mid-dorsal line is formed by autogenous (Mahajan, 1967b, p. 313; contra Regan, 1911) plates that are wider than long, each of which articulates with the expanded dorsal tip of its corresponding neural spine. The posteriormost mid-dorsal plate is twice as long as the others and bears a well-defined spine alongside the anterior margin of the adipose fin. Another series of plates extends on each side along the base of the dorsal fin. These plates are expansions of the distal portions of proximal dorsal fin pterygiophores and bear strong resemblance to the posterior nuchal plate. Therefore, the three series of bony plates in *Sisor* are formed in markedly different ways. It might be argued that the structural differences among the various series indicate three separate characters. This question is irrelevant for the present case because no member of the ingroup has only one or two of the three series, and a subdivision of the character would therefore be uninformative for hypothesized relationships.

Bony plates seem to have originated independently a number of times within siluriforms, namely in higher loricarioids (Callichthyidae, Scoloplacidae, Astroblepidae, and Loricariidae), Doumeinae (Amphiliidae), and Doradidae. In each
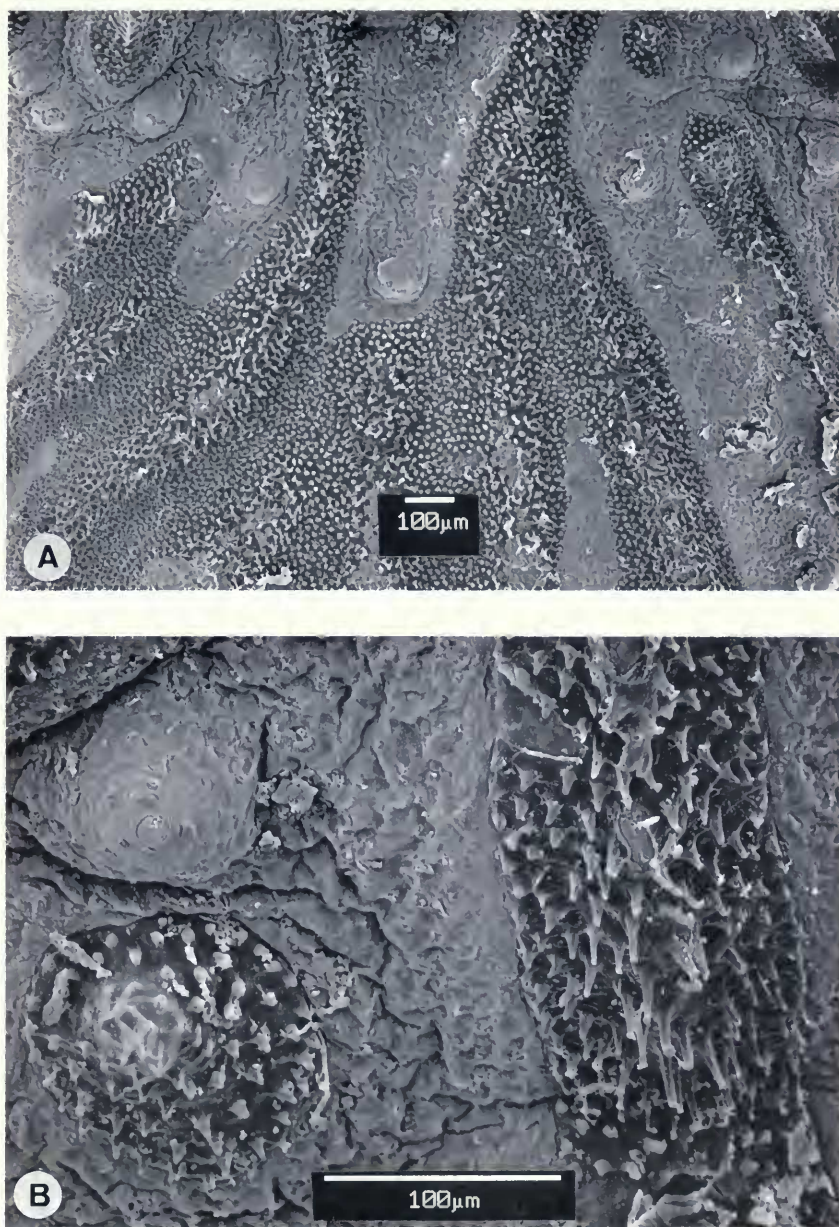
FIG. 50. *Conta conta,* UMMZ 208632, SEM photograph of adhesive apparatus, showing oblique folds (A) and unculi morphology (B).

of these groups, the hypotheses presently available (cf. de Pinna, 1993, and references therein) indicate that the armored clades are more closely related to naked taxa than to each other. The armored condition in *Sisor* is therefore hypothesized as uniquely derived.

112. First (uppermost) principal caudal fin ray enlarged and elongated as a filament (CI = 100).

Sisor.

The various principal caudal fin rays in siluriforms usually have a rather uniform morphology.
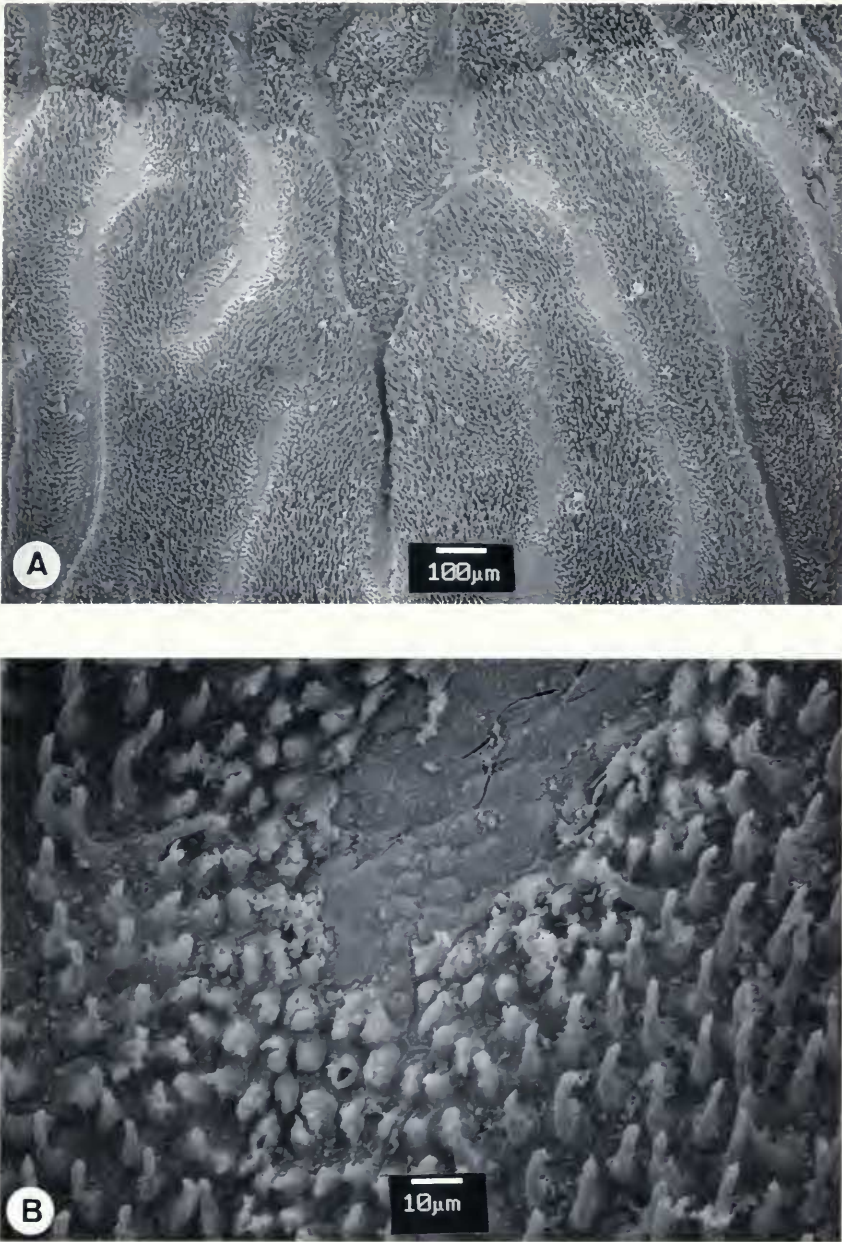
FIG. 51. *Laguvia ribeiroi,* UMMZ 208955, SEM photograph of adhesive apparatus, showing oblique folds (A) and unculi morphology (B).

Although their relative number and branching pattern may vary markedly among various taxa (Lundberg & Baskin, 1969), their size and structure change little from the uppermost to the lowermost ray in a single fin of an adult individual. In *Sisor,* the uppermost principal caudal fin ray is markedly enlarged (Mahajan, 1967b). The diameter of its proximal portion is about five times that of remaining rays, and its base covers over half the total area of the upper hypural plate. Additionally, the uppermost ray is elongated into a filament considerably longer than the standard length
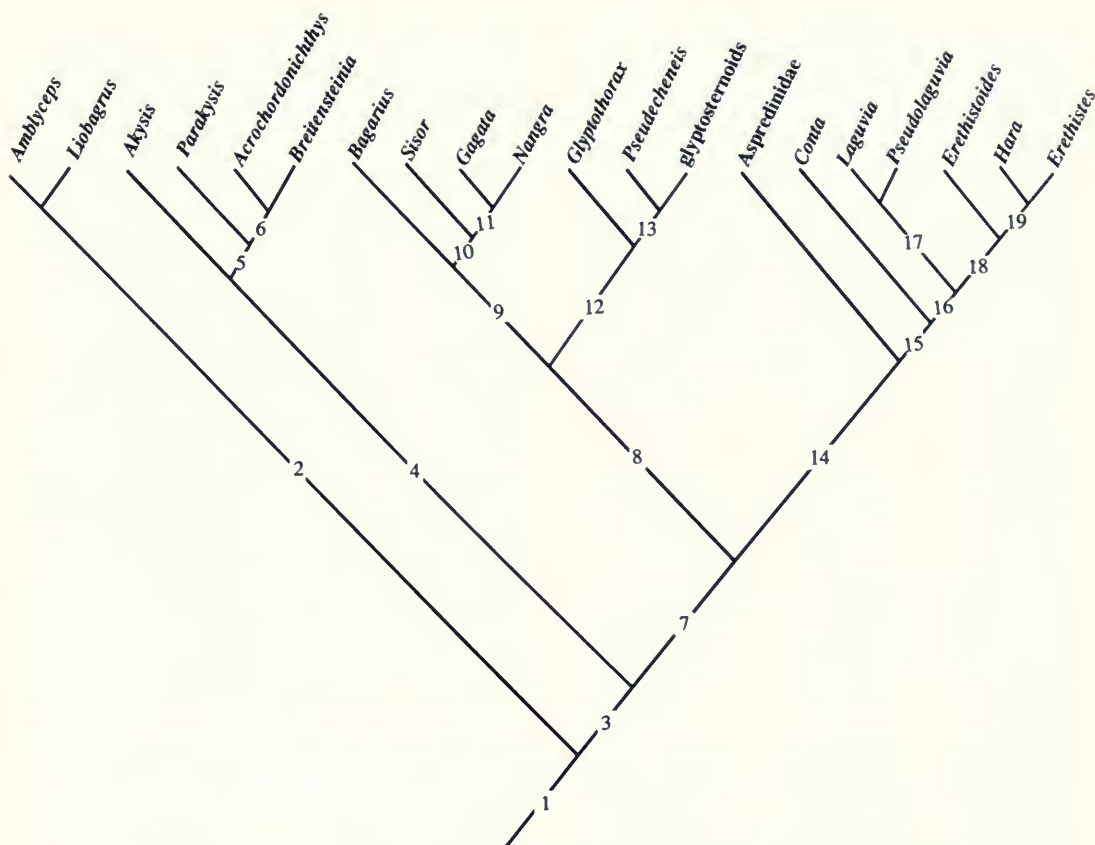
FIG. 52. Most parsimonious hypothesis of sisoroid relationships (CI = 70, RI = 79) based on 112 characters studied, with branches numbered. Characters transforming in each branch or terminal taxon are as follows. BRANCH 1: 1, 32, 61, 64, 77, 87, 91; BRANCH 2: 14, 20, 43, 51, 64, 76; BRANCH 3: 24, 26, 90; BRANCH 4: 13, 45, 64, 93, 98, 99; BRANCH 5: 2, 38, 41, 55, 72; BRANCH 6: 25, 33, 53; BRANCH 7: 27, 57, 62, 64, 66, 77 (reversal), 79, 87 (reversal), 88, 103; BRANCH 8: 30, 41, 60, 67; BRANCH 9: 4, 29, 63; BRANCH 10: 7, 8, 25, 44, 56, 109; BRANCH 11: 12, 34, 35, 41 (reversal), 92, 101; BRANCH 12: 49, 52, 110; BRANCH 13: 11, 24 (reversal), 27 (reversal), 57 (reversal), 59, 80, 81, 82, 89, 94; BRANCH 14: 3, 38, 84, 85, 97; BRANCH 15: 37, 54, 73, 86, 94, 110; BRANCH 16: 27, 58, 73; BRANCH 17: 19, 22, 41, 85 (reversal); BRANCH 18: 100; BRANCH 19: 65, 68; *Akysis*: 83, 95; *Parakysis*: 9, 15, 17, 18, 39, 40, 73, 76, 81, 98, 108; *Breitensteinia*: 71; *Bagarius*: 10, 21, 46, 50, 96, 105; *Sisor*: 3, 72, 84, 111, 112; *Gagata*: 69, 75; *Glyptothorax*: 10, 31; *Pseudecheneis*: 16, 36, 42, 70, 110; glyptoster-noids: 3, 5, 6, 41 (reversal), 64 (reversal), 78, 79 (reversal), 104, 110 (reversal); Aspredinidae: 23, 28, 47, 72, 93, 96, 99, 102, 103 (reversal), 106, 107; *Conta*: 74, 109; *Pseudolaguvia*: 48.

of the fish (Mahajan, 1967b). A certain degree of elongation of the uppermost principal caudal fin ray is not unusual in catfishes and other teleosts, being usually associated with deeply forked caudal fins. In cases where the upper lobe of the fin is elongated, the uppermost principal ray may be filamentous to a certain degree, such as in *Hara filamentosa* Blyth and in the genus *Conta* (cf. Hora, 1950). However, the condition of the uppermost ray in *Sisor* is unique in its extreme elongation and overall enlargement relative to the remaining caudal fin rays.

Phylogenetic Analysis

The 112 characters described above were coded for each terminal taxon, forming the data matrix shown in Table 1. This matrix was analyzed with the Hennig86 computer program (Farris, 1988). The exact algorithm ie found a single most par-simonious cladogram (Fig. 52), with a length of 167 steps, CI = 70, and RI = 79. An identical result was obtained using the much faster com-bination of heuristic algorithms mh*; bb*;. The same hypothesis was also encountered with PAUP

Table 1. Data matrix for superfamily Sisoroidea. Order of characters follows that presented and numbered in the text.

Hypothetical ancestor
0000000000 0000000000 0000000000 0000000000 0000000000 0000000000
0000000000 0000000000 0000000000 0000000000 0000000000 00
Acrochordonichthys
1100000000 0010000000 0001110000 0110000100 1000100000 0010100000
1002000000 0100001000 0000001001 1010000110 0000000000 00
Akysis
10000000?0 0010000000 0001010000 0100000000 0000100000 0000000000
1002000000 0000001000 0010001001 1010100110 0000000000 00
Breitensteinia
0100000000 0010000000 0001110000 0110000100 1000000000 0010100000
1002000000 1100000000 0000000001 1010000110 0000000000 00
Parakysis
1100000010 0000101100 0001010000 0100000111 1000000000 0000100000
100?000000 0120011000 1000001001 1010000010 0000000100 00
Amblyceps
1000000000 0001100001 0000000000 0100000000 0010000000 1000000000
1001000000 0000011000 0000001000 1000000000 0000000000 00
Liobagrus
1000000000 0001000001 0000000000 0100000000 0010000000 1000000000
1001000000 0000011000 0000001000 1000000000 0000000000 00
Bagarius
1001000001 0000000000 1001011011 0100000000 1000010001 0000001001
1113011000 0000000010 0000000101 1?00010000 0010100000 00
Conta
1?10000000 0000000000 0001011000 0100001100 0000000000 0001001000
1103010000 0011000010 0001110101 1001001000 0010000011 00
Erethistes
1000000000 0000000000 0001012000 0100001100 0000000000 0001001100
1103110100 0020000010 0001110101 1001001001 0010000000 00
Erethistoides
1000000000 0000000000 0001012000 0100001100 0000000000 0001001100
1103010000 0020000010 0001110101 1001001001 0010000000 00
Gagata
1001001100 0100000000 000111101? 0101100000 0001000000 0000011001
1113011010 0000100000 0000000101 1100000000 1010000010 00
glyptosternoids
1?1011000? 1000000000 0000010001 010000000? 0000000010 0100000011
1100011000 0000000101 1100000?11 1001000000 00?1000000 00
Glyptothorax
1000000001 0000000000 0001011001 1100000000 1000000010 0100001001
1103011000 0000000010 0000000101 1000000000 ?010000001 00
Hara
1000000000 0000000000 0001012000 0100001100 0000000000 0001001100
1103110100 0020000010 0001110101 1001001001 0010000000 00
Laguvia
1000000000 0000000010 0101012000 0100001100 1000000?0 0001001100
1103010000 0020000010 0001010101 1001001000 0010000001 00
Nangra
1001000100 0100000000 000111101? 0101100000 0000000000 0000011001
1113011000 00000000?0 0000000101 1100010000 1010000010 00
Pseudecheneis
1000000000 1000010000 0000010001 0100010000 1100000010 0100000011
1103011001 0000000011 1100000?11 1001000000 0010000002 00
Pseudolaguvia
1000000000 0000000010 0100012000 0100001100 1000000110 0001001100
1103010000 0020000010 0001010101 1001001000 0010000001 00
Sisor
1?10001100 0000000000 000111100? 0100000000 1001000000 0000011001
1113011000 0100000010 0001000?01 1000000000 00?0000010 11
Aspredinidae
1?1000?000 00000000?0 0011011100 0100000100 0000001000 0000001?00
1103010000 01?0000010 000?100?01 1010011010 0100011000 00

3.0 (Swofford, 1989). Statistics calculated with PAUP (length = 164, CI = 0.713, RI = 0.800) were slightly different from those calculated with Hennig86, supposedly as a result of the slightly different treatment of missing entries and non-additive (unordered) multistate characters. The tree was rooted with an all-zero hypothetical outgroup, representing a summary of the polarity assumptions discussed for each character above. The same most parsimonious unrooted network is obtained with or without the all-zero outgroup.

The robustness of the final result was tested first by an application of successive approximations weighting (Farris, 1969), implemented by the sequence of commands ie; xs w; cc; in Hennig86 and repeated iteratively until the assigned character weights stabilized (Fitzhugh, 1989). The application of successive weighting may result in a different tree even with data sets with a single most parsimonious solutions under an equal-weight analysis. In such cases, the procedure serves to reveal a subtle form of internal inconsistency in the data set. In the present case, however, the same result holds after successive approximations weighting.

Another test for the hypothesized relationships was the investigation of trees slightly longer than the most parsimonious tree(s) (so-called decay index or Bremer support; see review in Bremer [1994]). That procedure was implemented with PAUP. Eight trees were found with one extra step, and their semistrict consensus revealed a collapse of several components. Those that resisted collapse were composed of the taxa named below as Amblycipitidae, Acrochordonichthyini, clade B, Sisoridae, Sisorini, Nangrina, Glyptosterninae, Glyptosternini, Erethistidae, Laguviini, Erethistini, and *Hara* plus *Erethistes*. With two extra steps, 42 trees were found, and their semistrict consensus was similar to the previous one, except that within Sisoridae, only Nangrina and Glyptosternini resisted. With three extra steps, there were 182 trees, and only Amblycipitidae, clade B, Nangrina, Glyptosternini, and Laguviini were preserved. Nangrina collapsed at four extra steps (615 trees), and clade B disappeared at five extra steps (1,857 trees). The results of an analysis of component decay are difficult to interpret. Decay analysis can result in quick collapse of nodes even in data sets with no homoplasy, and a measure of clade robustness based on these procedures is dubious at best. The results obtained here are therefore offered for comparison with other studies than as an actual indication of clade support. Under the admittedly nebulous premise that the sequence of clade decay actually reflects some measure of clade robustness, one can make a number of inferences about relative support for groups. For instance, clade A, clade C, and Akysidae are the weakest among the major components, collapsing at a single extra step. This is particularly important in the case of clade C, which unites the Neotropical Aspredinidae with the Asiatic Erethistidae. Although the South American–Asian component is weak at that point, another component also supporting the same biogeographical relationship, clade B, is among the most resilient in the analysis, resisting up to four extra steps.

Classificatory Scheme

The single most parsimonious cladogram obtained in this analysis served as the basis for a new classification of the taxa studied. The main concern in translating the cladogram into a classificatory scheme was to minimize nomenclatural alterations of the currently adopted system. For that purpose, a combination of subordinating and sequencing conventions were adopted (see review by Wiley, 1981) so as to maintain names with their presently recognized rank and composition whenever possible. Nonetheless, a few changes of nomenclature were unavoidable because part of the favored phylogenetic hypothesis is directly incompatible with previous notions about the composition of some named groups. The single most important change is the placement of Aspredinidae as the sister group to a subset of current Sisoridae. Two viable options were considered in attempting to modify the previous classification so as to incorporate that information: (1) the current Sisoridae could be expanded to include the Aspredinidae, which could then be lowered to subfamilial rank, and (2) Aspredinidae could be maintained as a family, with Sisoridae split into two different families. I chose the second option, for a variety of reasons. First, there are very few siluriform families that are distributed on more than one continent, and among freshwater taxa none are found in both Asia and South America. Thus, maintaining the Neotropical Aspredinidae separate from the Asiatic Sisoridae would conform better to the current classification of the order. Second, an expanded Sisoridae (i.e., including current Sisoridae plus Aspredinidae) would be a rather difficult group to diagnose for practical purposes because of the large degree of morphological variation observed
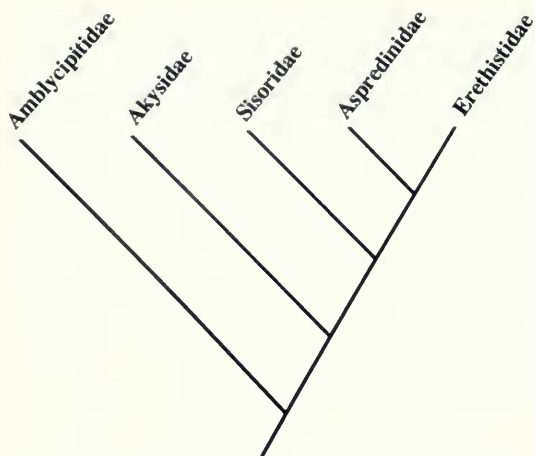
FIG. 53. Familial cladogram based on hypothesized relationships.

among its numerous members. A split into two families readily diagnosable by external morphology facilitates the making of keys for faunal surveys, manuals, and other identification tools.

Accordingly, the hypothesis in Figure 52 is translated into the familial cladogram represented in Figure 53, with Amblycipitidae, Akysidae, Sisoridae (*sensu stricto*), Erethistidae, and Aspredinidae arranged in this order as a sequenced classification. The scheme below also offers a classification down to tribal level for taxa so far included in Sisoridae and Akysidae, not only because these formed the main subject of this study but also because the hypothesis of relationships is resolved enough to allow that. The hierarchies below familial rank are all strictly subordinated. Figure 54 shows the relation between the most parsimonious cladogram in Figure 52 and the proposed familial and subfamilial classification.

The family Parakysidae, proposed by Roberts (1989) for *Parakysis* alone, is not maintained in

FIG. 54. Familial and subfamilial classification superimposed on most parsimonious cladogram.

the classification below. Instead, it is lowered to the rank of subfamily and modified to include also *Acrochordonichthys* and *Breitensteinia,* the closest relatives of *Parakysis.*

The assemblage composed of the five families is referred to as superfamily Sisoroidea. The first family names based on *Sisor* and *Aspredo* are available in the same publication (Bleeker, 1858). Sisoroidea was chosen over Aspredinidae simply because the former is listed first in Bleeker's classification. This is a rather arbitrary decision because the ICZN does not have a provision for line precedence of family-group names.

Superfamily Sisoroidea
  Family Amblycipitidae
  Family Akysidae
    Subfamily Akysinae
    Subfamily Parakysinae
      Tribe Parakysini
      Tribe Acrochordonichthyini, new
  Family Sisoridae
    Subfamily Sisorinae
      Tribe Sisorini
        Subtribe Sisorina
        Subtribe Nangrina, new
      Tribe Bagariini
    Subfamily Glyptosterninae
      Tribe Glyptosternini
        Subtribe Glyptosternina
        Subtribe Pseudecheneidina, new
      Tribe Glyptothoracini, new
  Family Erethistidae
    Subfamily Continae, new
    Subfamily Erethistinae
      Tribe Erethistini
      Tribe Laguviini, new
  Family Aspredinidae

Diagnoses for Clades and Synonymies for Named Taxa

This section summarizes the character information discussed in the previous sections, organized according to the most parsimonious hypothesis of relationships. The characters presented as diagnostic for each taxon are the apomorphic states of transitions optimized to occur at the node corresponding to that clade. Therefore, the list of diagnostic characters is technically a synapomorphy list. Accordingly, the diagnostic characters are not necessarily present in all the terminal taxa included in their respective clade. Any reversals and convergences of a given character are noted in parentheses. The numbering for diagnostic characters follows that in the "Character Description and Discussion" section above. Tracing of character transitions in the most parsimonious hypothesis was done with Clados 1.0 (Nixon, 1992). In cases of multiple equally parsimonious optimizations (i.e., ambiguous characters), the option that maximized reversals relative to convergences was chosen (de Pinna, 1991). The fact that a given character is ambiguous is, nonetheless, noted for each case.

Autapomorphies for terminal taxa are not included below (for a summary of autapomorphies, see Fig. 52). Diagnostic characters of a more practical nature are presented in the identification key in the next section.

Synonymies include the first published reference located for a given family-group name that meets current criteria of availability, followed by other selected publications relevant for the taxonomic history of the taxon. A list of genera included is provided for the lowest-level family-group taxon in each clade. These lists include only genera currently considered valid.

The diagnoses for Amblycipitidae and Aspredinidae should be regarded as provisional because these two families are currently the object of more in-depth studies by other authors.

Superfamily Sisoroidea
Bleeker, new usage

Synonymy—See Sisoridae below.

Families Included—Amblycipitidae, Akysidae, Sisoridae, Erethistidae, and Aspredinidae.

Diagnosis

1. Posterior center of ossification of palatine compressed and expanded vertically (reversal in *Breitensteinia*).
32. Articular region of lateral ethmoid elongated as a process, with articular facet for palatine at tip.
61. Parapophysis of fifth vertebra strong and attached to ventral side of centrum, directed directly transversely to centrum.
64. Humeral process or soft tissue around it connected to anterior portion of vertebral column by well-defined ligament (humerovertebral ligament).
77. Segments of pectoral fin spine very oblique, almost parallel to axis of spine, not evident

(reversed in *Breitensteinia* and clade B; alternative optimization possible).

87. Dorsal spine with medial ridges along its anterior surface, forming bilateral longitudinal pouches (reversed in clade B and *Breitensteinia*; alternative optimization possible).

91. Ventral tip of first dorsal fin pterygiophore and corresponding neural spines with contacting facets.

Family Amblycipitidae Day

Amblycepinae Day, 1873 (as subfamily of Siluridae).
Amblycepidae; Regan, 1911 (in part).
Amblycipitidae; Berg, 1940; Greenwood et al., 1966; Chardon, 1968; Jayaram, 1981; Burgess, 1989; Eschmeyer, 1990; Mo, 1991.

GENERA INCLUDED—*Amblyceps* Blyth, *Liobagrus* Hilgendorf, *Xiurenbagrus* Chen and Lundberg.

TYPE GENUS—*Amblyceps* Blyth, 1858.

DIAGNOSIS

14. Metapterygoid with well-defined thickening for ligamentous connection with ectopterygoid.

20. Hyomandibula with convex posterior expansion.

43. Second hypobranchial with longest axis nearly perpendicular to first.

51. Branchiostegal rays forming a closed, round arrangement.

64. Humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament (humerovertebral ligament)—state 1. Unordered character; status as evidence for monophyly uncertain.

76. First proximal radial elongated as a cartilaginous rod (convergent with Parakysini).

Unnamed Clade A
(Akysidae + Sisoridae +
Erethistidae + Aspredinidae)

DIAGNOSIS

24. Supratemporal fossae present (reversed in Glyptosternini and *Pseudolaguvia*).

26. Supracleithrum strongly attached to skull.

90. Posterior nuchal plate with anterior process forming facet for articulation with anterior nuchal plate.

Family Akysidae Gill

TYPE GENUS—*Akysis* Bleeker, 1858.

Akyses Gill, 1861 (as Group of the subfamily Pimelodinae).
Akyses; Bleeker, 1862 (as phalanx 9 of the Stirps Bagrini).
Akysidae; Weber and De Beaufort, 1913; Berg, 1940; Greenwood et al., 1966; Chardon, 1968; Jayaram, 1981; Burgess, 1989; Eschmeyer, 1990; Mo, 1991.
Parakysidae Roberts, 1989; Eschmeyer, 1990.
Amblycepidae (in part); Regan, 1911.

SUBFAMILIES INCLUDED—Akysinae, Parakysinae.

DIAGNOSIS

13. Metapterygoid with long anterior process (reversed in Parakysini; alternative optimization possible).

45. Anterior cartilage of anteriormost basibranchial enlarged (reversed in Parakysini; alternative optimization possible).

64. Humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament (humerovertebral ligament)—state 2 (reversed to 1 in Parakysini). Unordered character; status as evidence for monophyly uncertain.

93. First lateral-line ossicle enlarged, overlapping with posterior portion of supracleithrum (convergent in Aspredinidae).

98. Path of infraorbital laterosensory canal straight (reversal in Parakysini; alternative optimization possible).

99. Lacrimal with dorsal shelf-like portion directed mesially (convergent in Aspredinidae).

Subfamily Akysinae Gill

TYPE GENUS AND SYNONYMY—See Akysidae.
GENUS INCLUDED—*Akysis* Bleeker.

DIAGNOSIS

83. Anterior margin of pectoral fin spine with notch visible in dorsal view.
95. Nasal with expansions beyond canal-bearing portion.

Subfamily Parakysinae Roberts

TYPE GENUS—*Parakysis* Herre, 1940.

Parakysidae; Roberts, 1989; Eschmeyer, 1990.

DIAGNOSIS

2. Mandibular canal entering bone through its midsection (coded as missing in Aspredini-dae, *Sisor,* glyptosternoids, and *Conta*).
38. Second hypobranchial unossified (convergent in clade C).
41. Extra cartilaginous element anterior to last basibranchial (convergent in Sisoridae and Laguviini).
55. Posterior ceratohyal with dorsal process near its connection with suspensorium.
72. Vertebrae with transverse processes (convergent in Aspredinidae and Sisorina).

Tribe Parakysini Roberts

TYPE GENUS AND SYNONYMY—See Parakysinae.
GENUS INCLUDED—*Parakysis* Herre.
DIAGNOSIS

9. Posterior half of palatine twisted laterally (coded as missing in Akysinae).
15. Quadrate with anterior spur-like process (convergent in *Amblyceps*).
17. Metapterygoid reduced to its center of ossification.
18. Very large subpreopercle.
39. First hypobranchial unossified.
40. All basibranchials unossified (coded as missing in Glyptosternina).
73. Reduced number of pleural ribs, state 2 (convergent with Erethistidae and Erethistinae; coded as missing in Aspredinidae).
76. First proximal radial elongated as a cartilaginous rod (convergent with Amblycipitidae).
81. Humeral process absent (convergent with Glyptosternini).
98. Reversal to state 0 (alternative optimization possible).
108. Epural curved.

Tribe Acrochordonichthyini, new

TYPE GENUS—*Acrochordonichthys* Bleeker, 1858.
GENERA INCLUDED—*Acrochordonichthys* Bleeker, *Breitensteinia* Steindachner.
DIAGNOSIS

25. Paired fontanels between supraoccipital, frontals, and sphenotics (convergent in Sisorini).
33. Mesethmoid cornua with dorsal subdivision.

53. Proximal end of anterior ceratohyal with narrow anterior extension directed anterolaterally.

Unnamed Clade B
(Sisoridae + Erethistidae + Aspredinidae)

DIAGNOSIS

27. Posterior portion of supracleithrum ankylosed to margin of Weberian lamina (state 1; reversed to 0 in Glyptosternini; further modified as state 2 in Erethistinae).
57. Parapophysis of fifth vertebra strongly flattened and expanded (reversed in Glyptosternini).
62. Parapophysis of fifth vertebra long, almost or quite reaching lateral surface of body wall.
64. Humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament (humerovertebral ligament)—state 3 (reversed to 0 in Glyptosternina). Unordered character; status as evidence for monophyly uncertain.
66. Posterior part of Weberian lamina extensively contacting parapophysis of fifth vertebra.
77. [Reversal of] anterior half of segments of pectoral-fin spine elongate, almost parallel to axis of spine (alternative optimization possible).
79. Coracoid with ventral anterior process (reversed in Glyptosternina and *Gagata*; coded as missing in *Nangra*).
87. [Reversal of] second dorsal-fin spine with medial ridge along its anterior surface, forming bilateral longitudinal pouches (alternative optimization possible).
88. Ventral arms of first dorsal-fin spine with posterior subprocesses attached dorsal to their tip (coded as missing in Sisorina, all Glyptosternini, and Aspredinidae).
103. Basipterygium with ventral longitudinal keel, anteriorly extending alongside internal arm (reversed in Aspredinidae; coded as missing in Sisorina and Glyptosternina; ambiguous optimization possible).

Family Sisoridae Bleeker

TYPE GENUS—*Sisor* Hamilton, 1822.

Sisorichthyoidei Bleeker, 1858 (as Subfamilia I of Familia Siluroidei).

Sisoriformes; Bleeker, 1862, 1863 (as Subfamilia I of Familia Siluroidei).

Sisoridae; Gill, 1872; Regan, 1911; Berg, 1940; Greenwood et al.,. 1966; Chardon, 1968; Misra, 1976; Jayaram, 1981; Burgess, 1989; Eschmeyer, 1990.

Bagariidae; Weber and De Beaufort, 1913; Berg, 1940; Greenwood et al., 1966.

Sisolidae (misspelling); Kimura, 1934.

INCERTAE SEDIS—genus *Sundagagata* Boeseman, 1966.

SUBFAMILIES INCLUDED—Sisorinae, Glyptosterninae.

DIAGNOSIS

30. Lateral ethmoid with narrow lateral extensions directed posteriorly alongside lateral margin of frontals (coded as missing in all Sisorini).
41. Extra cartilaginous element anterior to last basibranchial (reversed in Nangrina and Glyptosternina; convergent in Parakysinae and Laguviini).
60. Distal tip of os suspensorum closely linked and/or adpressed to ventral process of complex centrum.
67. Posterior portion of Weberian lamina with lateral extension alongside anterior margin of parapophysis of fifth vertebra.

Subfamily Sisorinae Bleeker

TYPE GENUS AND SYNONYMY—See Sisoridae.
TRIBES INCLUDED—Sisorini, Bagariini.
DIAGNOSIS

4. Distal tip of maxilla pointed (reversed in *Sisor*; (alternative optimization possible).
29. Epioccipital with slender posterior process (reversed in *Sisor*; alternative optimization possible).
63. Posterodorsal corner of Weberian lamina with pointed process directed posteriorly.

Tribe Sisorini Bleeker

TYPE GENUS AND SYNONYMY—See Sisoridae.
SUBTRIBES INCLUDED—Sisorina, Nangrina.
DIAGNOSIS

7. Premaxillary dentition reduced or absent in adults (reversed in *Nangra*; coded as missing in Aspredinidae; alternative optimization possible).
8. Premaxillae with well-defined facet for articulation with mesethmoid.
25. Paired fontanels between supraoccipital, frontals, and sphenotics (convergent in Acrochordonichthyini).
44. Last basibranchial narrow (reversed in *Nangra*; alternative optimization possible).
56. Weberian capsule complete.
109. Stridulatory apparatus (state 2; state 1 convergent with Continae).

Subtribe Sisorina Bleeker

GENERA INCLUDED—*Sisor* Hamilton.
DIAGNOSIS

3. Mandibular laterosensory canal absent (convergent in Glyptosternina and clade C).
72. Vertebrae with transverse processes (convergent in Aspredinidae and Parakysinae).
84. Anterior margin of pectoral spine with serrations (convergent in Erethistidae and Aspredinidae).
111. Bony plates on surface of body.
112. First (uppermost) principal caudal fin ray enlarged and elongated as a filament.

Subtribe Nangrina, new

TYPE GENUS—*Nangra* Day, 1876.
GENERA INCLUDED—*Gagata* Bleeker, *Nangra* Day.
DIAGNOSIS

12. Direction of main axis of maxilla, when partly abducted, with strong ventral component.
34. Lateral ethmoid with well-defined dorsal facet contacting ventral surface of frontal.
35. Lateral ethmoid cartilage for palatine with extension for lacrimal.
41. [Reversal of] extra cartilaginous element anterior to last basibranchial.
92. Posterior nuchal plate straight and thin, its width approximately even from base to tip (coded as missing in Bagariini).
101. Dorsal half of suprapreopercle strongly curved posteriorly, making nearly 90° angle with ventral half (coded as missing in Glyptothoracini).

Tribe Bagariini Günther

TYPE GENUS—*Bagarius* Bleeker, 1853.

Bagarina Günther, 1864 (as the ninth group of subfamily Siluridae Proteropterae).

Bagarinae; Misra, 1976; Burgess, 1989.

Bagariidae (in part); Weber and De Beaufort, 1913; Berg, 1940; Greenwood et al., 1966.

GENUS INCLUDED—*Bagarius* Bleeker.
DIAGNOSIS

10. Distal portion of premaxilla detached (convergent in Glyptothoracini; coded as missing in Glyptosternina).
21. Endopterygoid with spur-like process anterolaterally.
46. Fourth ceratobranchial with tooth plates.
50. Proximal portions of epibranchials 1 and 2 adpressed to one another.
96. Nasal elongated anteriorly to level of anterior margin of mesethmoid cornua (convergent in *Nangra* and Aspredinidae).
105. Posterior cartilage of basipterygium ramified.

Subfamily Glyptosterninae Gill

TYPE GENUS—*Glyptosternon* McClelland, 1842. Glyptosterni Gill, 1861 (as Group of the subfamily Pimelodinae).
Glyptosterninae; Misra, 1976; Burgess, 1989.
TRIBES INCLUDED—Glyptosternini, Glyptothoracini.
DIAGNOSIS

49. Proximal portion of first and/or second epibranchial curved posteriorly (convergent in *Pseudolaguvia*; coded as missing in *Laguvia*).
52. Lateral wings of urohyal extremely reduced or absent.
110. Integument of thorax or thorax and abdomen modified into adhesive apparatus formed by patches of unculi underlain by ridges of integument (reversed to state 0 in Glyptosternina; further modified as state 2 in Pseudecheneidina; convergent in Erethistidae).

COMMENTS—A suprageneric name based on *Glyptosternum* was first proposed by Gill (1861) as Group Glyptosterni of the subfamily Pimelodinae. Although the family-group name has been formally available for over 130 years, it has almost never been used in Latin (exceptions: Misra, 1976; Burgess, 1989). Curiously, the collective name glyptosternoid sisorids, or simply glyptosternoids, has been widely cited in vernacular English to refer to the suprageneric group composed of *Glyptosternum* and its closest relatives (e.g., Hora & Menon, 1948; Hora & Silas, 1952a,b; Gauba, 1969; Steinitz, 1961; Tilak, 1963, 1976; Chu, 1979, 1981). Most uses of the vernacular name glypto-

sternoids are equivalent in composition to the taxon ranked below as subtribe Glyptosternina.

Tribe Glyptosternini Gill

TYPE GENUS AND SYNONYMY—See Glyptosterninae.
SUBTRIBES INCLUDED—Glyptosternina, Pseudecheneidina.
DIAGNOSIS

11. Presence of incisiform teeth on jaws.
24. [Reversal of] supratemporal fossae.
27. [Reversal of] posterior portion of supracleithrum ankylosed to margin of Weberian lamina.
57. [Reversed of] parapophysis of fifth vertebra strongly flattened and expanded.
59. Complex centrum as short as or shorter than free centra.
80. Eleven or more pectoral fin rays.
81. Humeral process absent.
82. Upper limb of cleithrum with laminar expansion directed mesially.
89. First dorsal fin ray flexible, not spinous.
94. Lacrimal modified into spoon-shaped structure located ventrolateral to nasal capsule (convergent in Erethistidae).

Subtribe Glyptosternina Gill

TYPE GENUS AND SYNONYMY—See Glyptosterninae.
GENERA INCLUDED—*Glyptosternon* McClelland, *Glaridoglanis* Norman, *Oreoglanis* Smith, *Exostoma* Blyth, *Myersglanis* Hora and Silas, *Coraglanis* Hora and Silas, *Euchiloglanis* Regan, *Pseudexostoma* Chu.
DIAGNOSIS

3. Mandibular laterosensory canal absent (convergent in Sisorina and clade C).
5. Maxilla dorsoventrally flat and strongly expanded distally.
6. Interopercle narrow and elongate, its laminar portion reduced.
41. [Reversal of] extra cartilaginous element anterior to last basibranchial (also homoplastically reversed in Nangrina).
64. [Reversal of] humeral region connected with anterior portion of vertebral column by well-defined ligament (reversal to state 0).
78. Proximal pectoral radials 2 and 3 flared at distal tip.
79. [Reversal of] coracoid with ventral process.

104. External arm of basipterygium abruptly expanded distally.
110. [Reversal of] integument of thorax or thorax and abdomen modified into adhesive apparatus formed by patches of unculi underlain by ridges of integument (reversed to state 0).

Subtribe Pseudecheneidina, new

TYPE GENUS—*Pseudecheneis* Blyth, 1860.
GENUS INCLUDED—Only the type genus.
DIAGNOSIS

16. Endopterygoid surrounding metapterygoid dorsally.
36. Sphenotic not contacting supraoccipital.
42. First epibranchial expanded anteriorly.
70. Dorsal expansion on first pleural rib.
110. Integument of thorax or thorax and abdomen modified into adhesive apparatus formed by patches of unculi underlain by ridges of integument (state 2).

Tribe Glyptothoracini, new

TYPE GENUS—*Glyptothorax* Blyth, 1860.
GENUS INCLUDED—Only the type genus (with three subgenera: *Glyptothorax, Paraglyptothorax* Li, and *Superglyptothorax* Li; Li, 1986).
DIAGNOSIS

10. Distal portion of premaxilla detached (convergent in Bagariini; coded as missing in Glyptosternina).
31. Lateral arms of vomer long and thin, extending underneath whole length of articular process of lateral ethmoid.

Unnamed Clade C
(Erethistidae + Aspredinidae)

DIAGNOSIS

3. Mandibular laterosensory canal absent (reversed in Erethistinae; convergent in Sisorina and Glyptosternina; alternative optimization possible).
38. Second hypobranchial unossified (convergent in Parakysinae).
84. Anterior margin of pectoral spine with serrations (convergent in *Sisor*; coded as missing in Aspredinidae).

85. Internal support for pectoral fin rays small in size (reversed in Laguviini).
97. Anterior portion of lateral line running closely in parallel to lateral margin of Weberian lamina.

Family Erethistidae Bleeker

TYPE GENUS—*Erethistes* Müller and Troschel, 1849.

Erethistides Bleeker, 1862, 1863 (as phalanx 10 of Stirps Bagrini).

SUBFAMILIES INCLUDED—Continae, Erethistinae.
DIAGNOSIS

37. Last hypobranchial with anterolateral extension.
54. Posterior margin of anterior ceratohyal with laminar expansion forming process directed laterally.
73. Five or fewer pleural ribs (convergent with Parakysini; coded as missing in Aspredinidae).
86. Extensive contact between expansions of first and second pterygiophores of dorsal-fin spines.
94. Lacrimal modified into spoon-shaped structure located ventrolaterally to nasal capsule (convergent in Glyptosternini).
110. Integument of thorax or thorax and abdomen modified into adhesive apparatus formed by patches of unculi underlain by ridges of integument (reversed in Erethistini; convergent in Glyptosterninae; alternative optimization possible).

Subfamily Continae, new

TYPE GENUS—*Conta* Hora, 1950.
GENUS INCLUDED—Only the type genus.
DIAGNOSIS

74. First two pleural ribs flattened and expanded.
109. Stridulatory apparatus (state 1 convergent with Sisorini).

Subfamily Erethistinae Bleeker

TYPE GENUS AND SYNONYMY—See Erethistidae.

TRIBES INCLUDED—Erethistini, Laguviini.
DIAGNOSIS

27. Posterior portion of supracleithrum anky-losed to margin of Weberian lamina (as state 2).
58. Parapophysis of fifth vertebra branched or notched distally (coded as missing in Aspredinidae).
73. Four or fewer pleural ribs—state 2 (convergent with Parakysini; coded as missing in Aspredinidae).

Tribe Erethistini Bleeker

TYPE GENUS AND SYNONYMY—See Erethistiidae.
GENERA INCLUDED—*Erethistes* Müller and Troschel, *Erethistoides* Hora, *Hara* Blyth.
DIAGNOSIS

100. Nasal adpressed to margin of neurocranium for two thirds or more of its posterior length, then abruptly diverging laterally at anterior portion.

Tribe Laguviini, new

TYPE GENUS—*Laguvia* Hora, 1921.
GENERA INCLUDED—*Laguvia* Hora, *Pseudolaguvia* Misra.
DIAGNOSIS

19. Opercle very narrow (coded as missing in Aspredinidae).
22. Endopterygoid bifurcated anteriorly.
41. Extra cartilaginous element anterior to last basibranchial (convergent in Sisoridae and Parakysinae).
85. [Reversal of] internal support for pectoral-fin rays small in size.

Family Aspredinidae Bleeker

TYPE GENUS—*Aspredo* Scopoli, 1777.

Aspredinoidei Bleeker, 1858 (as Familia II), 1862, 1863 (as Familia IV).
Aspredinina; Günther, 1864 (as 14th group, sixth sub-family—Siluridae Proteropodes).
Aspredinidae; Gill, 1872; Boulenger, 1904; Goodrich, 1909; Chardon, 1968; Nelson, 1994.
Bunocephalidae; Regan, 1911.

GENERA INCLUDED—*Amaralia* Fowler, *Xyliphius* Eigenmann, *Dysichthys* Cope, *Bunocephalus* Kner, *Agmus* Eigenmann, *Hoplomyzon* Myers, *Dupouyichthys* Schultz, *Ernstichthys* Fernández-Yépez.
DIAGNOSIS

23. Condyle for opercle on hyomandibula directed ventrally.
28. Pterotic with lateral shelf-like expansion.
47. Lateral cartilage of first hypobranchial enlarged.
72. Vertebrae with transverse process (convergent in Sisorina and Parakysinae).
93. First lateral-line ossicle enlarged, overlapping with posterior portion of supracleithrum (convergent in Akysidae).
96. Nasal elongated anteriorly to level of anterior margin of mesethmoid cornua (convergent in *Nangra* and Bagariini).
99. Lacrimal with dorsal shelf-like portion directed mesially (convergent in Akysidae).
102. Hyomandibula with bony tunnel enclosing branch of the laterosensory canal between preopercle and pterotic.
103. [Reversal of] basipterygium with ventral longitudinal keel, extending anteriorly alongside internal arm (coded as missing in Sisorina and Glyptosternina; alternative optimization possible).
106. Cartilage on posterior process of basipterygium reduced or absent.
107. Anterior arms of basipterygium undifferentiated from main part of bone.

Identification Key to Families Through Subtribes

This key has been elaborated as an aid to the implementation of the proposed changes in classification. The key is eminently practical and not intended to follow the branching sequence of the phylogenetic hypothesis advanced. Likewise, the characters used are not necessarily synapomorphies for the groups but rather are easily observed traits, of external anatomy whenever possible, that allow identification of taxa without the need for dissections or other more sophisticated preparations. Because the key is artificial, the user must keep in mind that certain taxa may have several different entries, and the key must be followed from the beginning each time.

1a. Adhesive apparatus, formed by integumentary ridges and grooves, present on thorax (between pectoral fins or immediately posterior to branchiostegal membranes) or abdomen 2
1b. Adhesive apparatus absent, skin of thorax and abdomen smooth 5
2a. Adhesive apparatus long and narrow, approximately 6 times or more as long as broad .... Erethistidae, Continae
2b. Adhesive apparatus shorter and broader than in 2a 3
3a. Grooves of adhesive apparatus transverse to longitudinal axis of body .... Sisoridae, Glyptosterninae, Glyptosternini, Pseudecheneidina
3b. Grooves of adhesive apparatus parallel or oblique to longitudinal axis of body 4
4a. Presence of a narrow bony area immediately posterior to and approximately as long as the humeral process, appearing to be a continuation of that process (not always visible on the surface of skin but evident to the touch .... Erethistidae, Erethistinae, Laguviini
4b. Area immediately posterior to tip of humeral process soft or, if bone is present, its length is far shorter than that of humeral process .... Sisoridae, Glyptosterninae, Glyptothoracini
5a. Humeral process poorly developed or absent, not visible through skin 6
5b. Humeral process well developed, visible through skin 7
6a. Pectoral fin rays 11 or more .... Sisoridae, Glyptosterninae, Glyptosternini, Glyptosternina
6b. Pectoral fin rays 9 or fewer .... Amblycipitidae
7a. Serrations absent on anterior margin of pectoral-fin spine 8
7b. Serrations present on both anterior and posterior margins of pectoral fin spine 9
8a. Prominent, semispherical, round skin tubercles over body 11
8b. Skin tubercles present either absent or, when present, flattened, ovoid in shape, and not prominent 13
9a. Broad bony plates present along mid-dorsal line posterior to dorsal fin .... Sisoridae, Sisorinae, Sisorini, Sisorina
9b. No bony plates as in 9a 10
10a. Adipose fin absent .... Aspredinidae
10b. Adipose fin present .... Erethistidae, Erethistinae, Erethistini
11a. Tip of pectoral fin, when adpressed to body, almost or quite reaching vertical through origin of pelvic fins .... Akysidae, Akysinae
11b. Tip of pectoral fin, when adpressed to body, not reaching vertical through origin of pelvic fins 12
12a. Skin tubercles arranged in longitudinal rows along body .... Akysidae, Parakysinae, Acrochordonichthyini
12b. Skin tubercles not arranged in longitudinal rows .... Akysidae, Parakysinae, Parakysini
13a. Flattened skin tubercles present .... Sisoridae, Sisorinae, Bagariini
13b. Skin tubercles absent .... Sisoridae, Sisorinae, Sisorini, Nangrina

Discussion and Comparison with Previous Classifications

The results of the phylogenetic hypothesis advanced herein help to settle a number of controversial issues about the systematics and taxonomy of the Sisoridae and their relatives. The genus *Laguvia* was created by Hora (1921) to include three species, *L. aspera* (the type species), *L. shawi,* and *L. ribeiroi,* the two latter described as new in the same paper. According to Hora (1921), *Laguvia* was in most respects intermediate between *Erethistes* and *Glyptothorax.* Later, the genus was placed as a synonym of *Glyptothorax* by Menon (1954),

a move subsequently accepted without comment by Li (1986). Menon's reason for his action was that the characters given by Hora to distinguish *Laguvia* from *Glyptothorax* were minor and were actually present in some species of the latter. Menon particularly noted the similarities between *Laguvia* and *Glyptothorax tuberculatus,* a species later made the type of a separate genus, *Pseudolaguvia,* by Misra (1976). The genus *Laguvia* was resurrected by Gauba (1970b), who studied the internal anatomy of the genus and recorded a number of similarities between *Laguvia* and *Glyptothorax* and between *Laguvia* and *Erethistes.* Comparing the evidence for the alternatives, Gauba decided that there was more support for grouping

Laguvia and *Erethistes* and further suggested that the synonymy of *Laguvia* under *Glyptothorax* proposed by Menon (1954) was incorrect. Gauba (1967, 1970b) informally recognized a natural group similar to the family Erethistidae as defined in the present study and on occasion even used the vernacular "erethistid" (e.g., Gauba, 1970b, p. 63). Apparently unaware of Gauba's previous work, Jayaram (1973) also proposed to revalidate *Laguvia* and further suggested that the genus was most closely related to *Hara*. Again without reference to Gauba, Tilak (1976) also informally recognized a relationship between *Laguvia* and *Erethistes*-like taxa when he said that "the fishes of the genus *Laguvia* tend to show more affinities to the *Erethistes* group of sisorid fishes" (Tilak, 1976, p. 259). The suggestions of Gauba, Jayaram, and Tilak, although not formulated within a strictly comparative phylogenetic framework, are corroborated by the results of this study. Numerous apomorphic characters support the position of *Laguvia* (and the closely related *Pseudolaguvia*) in an internested subset of Erethistidae. Menon's (1954) previous suggestion of synonymy evidently had been based on a sense of overall similarity between *Laguvia* and *Glyptothorax*, which turns out to consist only of symplesiomorphies. Günther (1864) and Bleeker (1873) included *Pimelodus asperus* (later the type species of *Laguvia*) in *Hara,* a placement that is close to the actual phylogenetic affinities of the genus.

A controversy about the distinctiveness of *Gagata* and *Nangra* (cf. Hora & Law, 1941; Tilak, 1963) is also affected by the hypothesis presented in this paper. These two genera are hypothesized as sister groups on the basis of a large set of synapomorphies. Although only a few species of each genus were examined, preliminary evidence suggests that each forms a monophyletic group. In this situation, the question of their generic separation becomes rather irrelevant because both alternatives are compatible with the proposed phylogenetic relationships. I agree with Tilak (1963) that the morphological distinctions between *Nangra* and *Gagata* are at least as pronounced as those among most other genera in Sisoroidea. Hora and Law's suggestion of synonymy was not based on a detailed knowledge of the internal anatomy of these fishes and relied mostly on their smaller external morphology.

The phylogenetic affinities of the genus *Pseudecheneis* have also been controversial. Early studies pointed out similarities and differences between that genus and various "glyptosternoid si-

sorids" but were not conclusive about their possible phylogenetic affinities (Hora & Chabanaud, 1930; Hora, 1952; Hora & Silas, 1952a,b). Various speculations about convergent morphology of the adhesive apparatus adaptations led to the recognition of *Parapseudecheneis* (Hora & Chabanaud, 1930) and *Propseudecheneis* (Hora, 1937). Hora and Chabanaud (1930) proposed that *Pseudecheneis* and *Parapseudecheneis* were derived from different lineages within glyptosternoids. Essentially the same view was reiterated by Hora (1952) but with the addition of one more allegedly convergent lineage represented by *Propseudecheneis*. In any case, the origin of *Pseudecheneis, Parapseudecheneis,* and *Propseudecheneis* was considered to be within the glyptosternoid lineage, therefore implicitly indicating that the whole assemblage (glyptosternoids plus the three genera) formed a monophyletic group. Both *Parapseudecheneis* and *Propseudecheneis* were later considered junior synonyms of *Pseudecheneis* by Chu (1982), who proposed that the three genera formed a monophyletic group, thus refuting Hora's convergence hypothesis. Of the three putative synapomorphies proposed by Chu (1982, p. 435) for the expanded *Pseudecheneis,* two can be considered valid evidence for monophyly: the structure of the adhesive organ and the lack of contact between the sphenotic and supraoccipital (his characters nos. 11 and 13, respectively, the latter originally proposed by Gauba [1968, p. 233]; a third character, the absence of a dorsal fin spine [Chu's no. 12], is actually a synapomorphy for glyptosternoids plus *Pseudecheneis*). Although these two characters are reliable evidence for monophyly, the internal anatomy of the most distinctive species, *P. paviei,* remains unknown, therefore leaving the structure of the adhesive organ as the only derived character observed in all species of *Pseudecheneis.* Regardless of these limitations, the monophyly of *Pseudecheneis* is a reasonable working hypothesis, although one that needs further testing. Chu (1982) focused exclusively on the problem of the monophyly of *Pseudecheneis* and did not address the question of that genus's closest relatives. Tilak (1976, p. 260) proposed a close relationship between *Pseudecheneis* and glyptosternoids, mainly on the basis of an overall similarity in their pectoral spine morphology. In support of Tilak's view, a large set of synapomorphies advanced in the present study support the alignment of *Pseudecheneis* with the glyptosternoid group of sisorids. These characters plus the numerous synapomorphies exclusive to glyptosternoids leave little doubt

that *Pseudecheneis* is the sister group of glypto-sternoids. In certain ways, *Pseudecheneis* is less specialized for torrential life than are glyptoster-noids, as has been repeatedly observed (e.g., Hora and Silas, 1952a). From the phylogeny advanced herein, it is clear that the fewer specializations of *Pseudecheneis* are a result of the basal position of that genus rather than a reversal from a more ex-treme condition. Thus, the adaptations to torren-tial environments observed in *Pseudecheneis* are structurally and phylogenetically intermediate be-tween those of *Glyptothorax* and glyptosternoids.

A familial separation between the Akysidae and the Amblycipitidae has been recognized since We-ber and de Beaufort (1913). Prior to that, fishes now included in Akysidae were part of a broader Amblycipitidae (e.g., Regan, 1911). In delimiting his Amblycepidae [sic], Regan (1911) considered similarities in the edentulous palate and anterior vertebrae between *Akysis* and *Acrochordonichthys* and between *Amblyceps* and *Liobagrus*. None of these resemblances, however, can be considered putative synapomorphies by today's standards. Hora (1936) discussed this problem and concluded that the morphological differences justified rec-ognition of a separate Akysidae. Although Hora's reasoning relied on degree of difference rather than genealogical kinship, his conclusions are essen-tially correct in a phylogenetic context. The most parsimonious hypothesis favored in this work in-dicates that members of the Akysidae and Am-blycipitidae are not each other's closest relatives. Recognition of an expanded Amblycipitidae in Regan's sense would result in a paraphyletic as-semblage, thus requiring a separate Akysidae, as adopted in most classifications of this century.

Some of the results above will likely be shown to be incomplete under a more fine-grained anal-ysis because of incomplete representation of spe-cies in the studied taxa. In particular, the genera *Akysis* and *Glyptothorax* may be deemed para- or polyphyletic in more encompassing studies. The genus *Akysis* comprises approximately 10 de-scribed species (He & Chen, 1981), but only four were available for examination here. Two char-acters (81 and 91) were found to corroborate that these four species compose a monophyletic group. Some species currently in *Akysis* may be more closely related to species in other akysid genera. For example, character 9 is shared between *Par-akysis* and only some *Akysis* species. Such syna-pomorphies should serve as indicating that the monophyly of *Akysis* should not be taken for granted in more complete studies on the genus.

Species in *Akysis* probably compose an assemblage far more complex and diverse than so far realized, a complexity that has not yet been recognized be-cause of the rarity of representatives of the genus in collections.

The genus *Glyptothorax* also is probably com-plex, and the hypothesis proposed herein for the position of the taxon may be quite incomplete. One uniquely derived character (no. 31) for the genus was observed in all representatives available for examination or for which published data were available. However, the condition of this character in most of the approximately 40 species of *Glyp-tothorax* remains to be determined. A second char-acter transition is also hypothesized to be apo-morphic for *Glyptothorax* (character 10), but this character is homoplastic with other clades. If the genus is actually shown to be nonmonophyletic, it is unlikely that its species will be spread through-out widely diverging levels of sisorid phylogeny. Most probably they will be restricted to the Glyp-tosterninae, some of them perhaps as sister group to the whole subfamily or to the tribe Glyptoster-nini. One interesting feature too poorly known to be included in the character analysis but which deserves discussion is a peculiar foramen found in the pterosphenoid. The lateral portion of the braincase in *Pseudecheneis* is remarkably com-plex, with a number of foramina and subdivisions not observed in other siluriforms. Of particular relevance is the foramen formed by a roughly Y-shaped posteroventral process of the pterosphe-noid. The arms of the process are widely divergent at the base and then curve strongly toward each other, forming a well-defined, rounded space in the center. The foramen thus formed is actually located in the area corresponding the prootic but is enclosed by ossifications derived from the pter-osphenoid. Such a configuration is certainly de-rived for siluriforms and is seen also in remaining members of the Glyptosternini, although in a somewhat modified form. A very similar situation is found in some of the species examined of *Glyp-tothorax,* such as *G. major,* but not in others, such as *G. sinense.* This may indicate that some species of *Glyptothorax* are more closely related to species of other genera in the Glyptosternini than to other species currently in *Glyptothorax.* Evidently there is some character incongruence involved in the situation because the species of *Glyptothorax* in question share a derived character not seen else-where in the Glyptosternini. Solution of this prob-lem will have to await a more complex study of *Glyptothorax,* a genus in urgent need of a species-

level revision and smaller-scale phylogenetic treatment.

There is also some indication that the genera *Gagata* and *Nangra* may be nonmonophyletic as presently constituted. A striking synapomorphy was found for two species, one from each genus. The posterior portion of the palatine in *Nangra nangra* and *Gagata cenia* is expanded dorsoventrally to an extreme degree (Fig. 55). This expansion goes far beyond the normal synapomorphic condition of that bone in sisoroids (cf. character 1) and is evidently a character exclusive to those two species among the taxa examined. This extreme condition of the palatine expansion is not present in the remaining species examined of both *Gagata* and *Nangra* and thus may indicate that neither genus is monophyletic. Again, both genera include a number of species not available for examination in the present study, but present evidence hints at a rather complex systematic situation involving *Gagata* and *Nangra*.

Two patterns of homoplasy are noteworthy in this study. The first is the set of synapomorphies for aspredinids and akysids. The most conspicuous of these is the presence of large vertebral transverse processes, which sometimes extend all the way to the body surface (character 72). This character is also homoplastically present in *Sisor*. In that taxon, however, the processes are associated with the bony plates derived from lateral-line ossicles and clearly provide partial mechanical support for them. This situation does not occur in akysids and aspredinids, where there are no bony plates on the surface of the body. This structural–functional difference, when interpreted in light of the phylogenetic hypothesis, provides a posteriori evidence that the transverse processes in *Sisor* are not homologous to those in other sisoroid taxa. The structure of the transverse processes in aspredinids and akysids, however, is very similar and is only revealed as homoplastic by the topology of the most parsimonious cladogram. Additional synapomorphies for aspredinids and akysids are the enlarged first lateral-line ossicle, which is also adjoined to the posterior portion of the supracleithrum (character 93), and the morphology of the lacrimal, which has a dorsal shelf-like portion directed mesially (character 99). Again, no structural detail seems to indicate, even a posteriori, that the conditions of these traits are non-homologous in akysids and aspredinids. Their homoplastic condition is a conclusion stemming only from parsimony considerations.
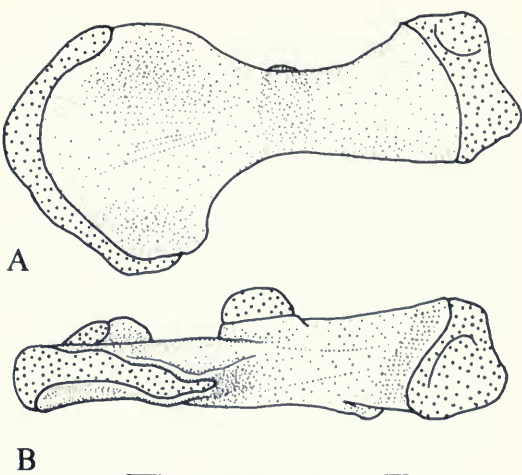
Another noteworthy pattern of homoplasy is ob-

FIG. 55. *Nangra nangra*, CMK 6369, right palatine. **A**, lateral view. **B**, ventral view. Larger stippling represents cartilage. Scale bar = 1 mm.

served between *Parakysis* and amblycipitids. The morphology of the first proximal pectoral radial in *Parakysis* and amblycipitids is very similar (character 76), having the shape of an elongate cartilaginous rod unique among sisoroids and very distinctive from the plesiomorphic condition in most other siluriforms. Fitting the same pattern, the presence of a spur-like process on the quadrate (character 15) occurs exclusively in *Parakysis* and *Amblyceps* (but not in *Liobagrus*). The state of the humerovertebral ligament (character 64) should also be mentioned in this regard. *Parakysis* and amblycipitids are the only taxa in which the ligament is not attached to the humeral process. Although the ordering of the three states of the humerovertebral ligament is as yet undetermined, as is the correct coding for the character in *Parakysis*, the distribution of the various states in the most parsimonious scheme leaves little doubt that any derived similarities found in that complex for *Parakysis* and amblycipitids are homoplastic because *Parakysis* is adjacent to two clades showing state 2 for character 64 (*Akysis* and *Breitensteinia* + *Acrochordonichthys*).

An additional similarity between *Parakysis* and amblycipitids that was not included in the data analysis is the shape of the endopterygoid. In both taxa, the bone has the shape of an inverted L, with its anterior portion strongly deflected laterally, forming roughly a 90° angle with the posterior portion of the bone. The endopterygoid is much smaller in *Parakysis* than in the amblycipitids, but

the similarity in general shape is undeniable and is certainly derived within siluriform. The problem with this similarity is the state assignment to other terminal taxa in the Sisoroidea. The endopterygoid is present in all of them, and in several cases it has a shape similar to that in *Parakysis* and amblycipitids, although with a broader ossified area. In some cases, the L shape of the endopterygoid is simply obscured by additional ossification. A comparison of various endopterygoids shows that there are conditions in which the L shape is clearly present, others in which it is identifiable but poorly defined, and a few in which it is not present by any stretch of the imagination. Examination of early ontogenetic stages in members of the ingroup may reveal that the L-shaped endopterygoid is actually present in a large subset and that it is subsequently obscured by additional bone expansions in adult individuals of most ingroup taxa. Such ontogenetic data are presently unavailable, but without them we cannot adequately understand and code this character. With present information, the addition of this character to the data matrix would result in an unacceptably large number of taxa with the character coded as missing, which in turn would obscure more information than it would reveal. For these reasons, the similarity in endopterygoid shape between *Parakysis* and amblycipitids is considered a character impossible to adequately delimit with current knowledge and accordingly was left out of the parsimony analysis.

Comments on Miniaturization and Gigantism in Sisoroidea

The evolutionary and ecological significance of miniaturization in vertebrates has been discussed in a number of recent publications. For freshwater fishes, Weitzman and Vari (1988) and Kottelat and Vidthayanon (1993) provided lists of miniaturized species known from South America and South or Southeast Asia, respectively. Both publications adopted an arbitrary maximum of 26 mm standard length (SL) for a species to be considered as a miniature. Weitzman and Vari (1988), however, recognized that this cutoff is simply a first approximation and that numerous other traits characterize miniaturized species, some of which may exceed that length. Sisoroidea includes the only truly miniaturized catfish reported in South Asia (the erethistid *Erethistes maesotensis* Kottelat, according to Kottelat & Vidthayanon, 1993).

Other Asiatic taxa that are obviously miniatures, even though they may on occasion slightly exceed 26 mm SL, are *Hara jerdoni* (Day) and all species included in *Laguvia* and *Pseudolaguvia* (of Erethistidae). Other recognized sisoroid miniatures occur in the tribe Hoplomyzontini (Aspredinidae: *Dupouyichthys sapito* Schultz and *Hoplomyzon papillatus* Stewart; Weitzman & Vari, 1988).

At the other extreme, sisoroids also include one gigantic species, the sisorid *Bagarius yarrelli*. This species is reported to reach close to 2 m in length (Roberts, 1983, 1989) and is one of the largest catfishes in Asia.

It has been repeatedly observed that paedomorphic traits commonly present in miniatures tend to occur in identical form in phylogenetically unrelated lineages (Weitzman & Vari, 1988; Schaefer et al., 1989; Begle, 1991; Grande, 1994). Such traits include various reductions in the laterosensory canal system, number of fin rays, and degree of ossification. In some instances, reductions are carried on to total absence of certain structures. Anatomical changes associated with gigantism seem to be far less profound than those related to miniaturization. This is not surprising, because reduction in size is nearly always associated with a truncation of ontogeny, an association not occurring in cases of phylogenetic size increases. Most of the morphological alterations typically undergone by gigantic species seem to involve an increased degree of ossification, often resulting in thicker bones and tighter sutures. Although these changes may in some cases obscure some osteological characters, their underlying condition can usually still be observed in half-grown individuals. From the viewpoint of phylogenetic reconstruction, problems in character coding related to gigantism are far less critical than those related to miniaturization.

All miniature sisoroids are in the families Erethistidae and Aspredinidae. The usual way to assess the number of miniaturization events in a group is to treat miniaturization as a character and optimize it on the most parsimonious tree topology. The number of independent origins plotted on the tree is the number of miniaturization events hypothesized to have occurred in the clade. On the cladogram advanced in this study, miniaturizations within erethistids probably occurred at least twice: once in the *Laguvia* + *Pseudolaguvia* clade (tribe Laguviini) and once within the *Hara* + *Erethistes* clade. Miniaturization in this clade, involving *Hara jerdoni* and *Erethistes maesotensis,* is here conservatively considered as a single

event. Although the hypothesis that *Erethistes* and *Hara* form a monophyletic group is well corroborated, there is no evidence that either genus is monophyletic as presently constituted. Both genera are in need of revision and a fine-grained phylogenetic treatment. At present, there is no clear reason to discard the possibility that *E. maesotensis* and *H. jerdoni* are sister groups, despite their present allocation to different genera, and therefore accountable for by a single miniaturization event. This reasoning is in accordance with the purpose of assessing only the minimum number of miniaturization events.

The two miniaturized species within hoplomyzontin aspredinids have been hypothesized to represent independent miniaturization events (Weitzman & Vari, 1988, p. 456). Although those species are the smallest in the family, the whole tribe Hoplomyzontini can be considered miniaturized under a less restrictive definition of the term. All hoplomyzontines are very small in body size and have reductions in the laterosensory canal system and in the number of fin rays.

The taxa phylogenetically close to miniaturized sisoroid clades are all of small size. All erethistids have small overall body size, and their closest relatives, the aspredinids, show a similar pattern. The only medium-sized aspredinids are the few species in the subfamily Aspredininae. However, all aspredinines have a markedly elongated caudal region, which accounts for a large part of their SL and thus obscures the actual size condition of other body regions. This effect is similar to that referred to by Weitzman and Vari (1988) as elongated miniatures, when truly miniaturized species exceed a certain SL because of an elongated body shape.

In contrast, the lineage that includes the gigantic *Bagarius yarrelli* comprises several species of medium size. Among its closest relatives, *Sisor* and some species of *Gagata* can reach beyond 200 mm SL, a size unknown in erethistids. The same is true of Glyptosterninae, where some *Glyptothorax, Pseudecheneis,* and Glyptosternina may reach 200 mm SL. Similarly, other species of *Bagarius* are also medium-size to large fishes, with *B. bagarius* reaching 192 mm SL and *B. suchus* reaching 515 mm SL (Roberts, 1983).

These observations indicate that both miniaturization and gigantism are not abrupt events in the phylogenetic context for these groups. Extreme modifications of body size, toward either increase or decrease, seem to occur gradually across lineages. The definitions of miniaturization and gigantism apply to the most extreme cases of what

seems to be a gradual phenomenon. Although detailed comparative data are not available, it seems that this rule applies to other catfish groups as well. All miniaturized members of the Neotropical family Trichomycteridae (Weitzman & Vari, 1988; de Pinna, 1989) belong to clades in which most or all species have small body size. The only miniaturized loricariid (*Microlepidogaster lophophanes* (Eigenmann and Eigenmann)) is a member of a subfamily (Hypoptopomatinae) where most species are small relative to the remainder of the family. Similarly, the various miniaturized callichthyids (Weitzman & Vari, 1988) are all related to small members of the family (Reis, 1993). How well other miniature siluriforms (and other fish groups) fit into this pattern still needs to be determined.

Data on gigantism are far less extensive than those on miniaturization because fewer species fit in the former category. Preliminary observations, however, seem to indicate that a pattern similar to that in Sisoridae occurs in the Asiatic Pangasiidae and the Neotropical Pimelodidae. There are at least two pangasiid species that unquestionably qualify as gigantic—*Pangasius gigas* and *P. sanitwongsei,* both reported to reach 3 m SL and 300 kg (Roberts & Vidthayanon, 1991). Little is known about the phylogenetic position of *P. sanitwongsei,* but the closest relative of *P. gigas* is probably *P. hypophthalmus* (Durand, 1949; Roberts & Vidthayanon, 1991), a species reaching at least 80 cm SL and 7 kg, and perhaps up to 1.3 m and 15.5 kg (Roberts & Vidthayanon, 1991). Pangasiidae includes exclusively medium-sized to large fishes, with most of them reaching beyond 50 cm SL as adults, several reaching 80 cm SL, and the smallest to ca. 20 cm SL (Roberts & Vidthayanon, 1991). Within pimelodids, one member of the subfamily Sorubiminae is reported to reach beyond 2 m SL and 100 kg (e.g., *Brachyplatystoma filamentosum;* see Goulding, 1980). All other members of the Sorubiminae, probably a monophyletic group, are all medium or large in size, many of which reaching beyond 1 m SL as adults.

Evolution of the Sound-producing Apparatus in Sisoroids

The remarkable sound-producing apparatus present in *Sisor, Gagata, Nangra,* and *Conta* has been described above as character 109. The first published account of this complex was by Haddon (1881), who described its structure in *Gagata* (=

Callomystax). The same observations were repeated by Bridge and Haddon (1893), and later a very similar sound-producing apparatus was reported in *Sisor* by Mahajan (1963). Tilak (1963) briefly recorded the presence of a stridulatory apparatus in *Gagata gagata* and *Nangra viridescens* and reported its absence in the closely related *Nangra punctata*.

The sound-producing ability of the stridulatory apparatus in the living fish has been reported only in *Sisor* (Mahajan, 1963), but the anatomical similarities of this apparatus in other taxa makes it likely that the mechanism plays a similar role in all of them. The sound emission is at least in part related to defense; Majahan (1963; p. 723) reported that "[*Sisor*] produces a very distinct and audible sound when caught in the aquarium and the intensity of sound increases considerably when the fish is taken out of water." Mahajan also noted that the sound produced by the fish was similar to that produced by manipulating the stridulatory apparatus of preserved fish. Whether the same stress reaction is displayed by *Gagata, Nangra,* and *Conta* remains to be investigated.

The degree of development of the stridulatory apparatus varies among species. In *Gagata* and *Sisor,* it is always well developed and heavily ossified. The same is true for *Nangra viridescens*. In *N. nangra,* however, all elements of the apparatus are weak and thinly ossified, and the ridges are few and poorly differentiated. Nonetheless, the whole skeleton in that species is slight and thinly ossified, indicating that the reduced condition of the stridulatory apparatus is part of a trend toward reduction throughout the whole skeletal system in that species and not a reduction of the mechanism per se. Also in *N. nangra,* the ridged surfaces of the supraneural (= first nuchal plate) are not tightly united into a solid structure as in *N. viridescens, Gagata,* and *Sisor.* The same situation observed in *N. nangra* probably occurs in *N. punctata,* judging from illustrations by Tilak (1963, p. 305, Figs. 46, 47). The neural spine of the complex centrum in *N. punctata* is broad at the tip, a condition typical of species with a stridulatory apparatus. As in *N. nangra,* the ridged surfaces in *N. punctata* probably are rather attenuated and visible with clarity only at certain angles and considerable magnification.

The morphological modifications of the dorsal fin elements involved in the basic functioning of the stridulatory mechanism are very similar in all taxa and leave little room for an a priori hypothesis of nonhomology. In the phylogenetic hypothesis advanced here, *Sisor, Nangra,* and *Gagata* form a monophyletic group and the presence of the sound-producing mechanism is a synapomorphy (i.e., homologous) for that clade. However, a stridulatory apparatus based on a similar set of anatomical modifications and resulting in a very similar functional complex occurs in the genus *Conta.* Here, the apparatus is likewise formed by modifications of the skeletal elements associated with the dorsal fin (first nuchal plate) and complex centrum, and the sound-producing mechanism relies on the same overall physical basis, that is, a series of fine bony ridges on opposing surfaces. I assume a priori, based on a number of anatomical similarities (see description and discussion of character 109), that the conditions observed in *Sisor, Nangra,* and *Gagata* and those observed in *Conta* are homologous. Although that assumption may be the most reasonable course of action in view of the data available, assumptions about morphological homology (the primary homologies of de Pinna, 1991) involve an element of subjectivity that may be critical in certain situations. There are borderline situations where two or more structures are neither similar enough to unquestionably be considered homologous nor distinct enough to be considered nonhomologous. In a certain way, the stridulatory apparatus is in this category.

In the phylogenetic hypothesis presented here, the *Sisor/Gagata/Nangra* clade (tribe Sisorini) is a number of nodes apart from *Conta* in the cladogram, and this topology leaves no room for considering the derived similarities in sound-producing abilities as homologous in the two lineages. This result holds despite the initial working assumption, encased in the character coding used to build the data matrix, that the stridulatory mechanism is a primary homologue in *Conta* and Sisorini. Thus, some of the differences between the stridulatory apparatus in *Conta* and Sisorini can be interpreted a posteriori as evidence of nonhomology. The most obvious distinction is the plane of the ridged surfaces, nearly horizontal in *Conta* and vertical in Sisorini. Also, in Sisorini there is a trend toward approaching the ridged surface of either side of the supraneural, often forming a single median vertically ridged sphere. In *Conta,* there is an opposite tendency, with the crenulated surfaces of the supraneural positioned wide apart and rather independent of one another except for their attachment on the same supraneural. Although these differences in themselves are not grounds for discarding the primary homology of the stridulatory apparatus in Sisorini and *Conta,* they may

gain relevance under the available phylogeny, once the ontogeny of the different varieties of the mechanism become known. A hypothesis of nonhomology would be supported if it is found that neither version of the apparatus is a stage in the development of the other, i.e., that they derive independently from a condition similar to that in generalized sisoroids (see below). Based only on adult morphology, it is impossible to objectively establish transformation series for the two states of the stridulatory apparatus. Both seem to be highly divergent from the plesiomorphic sisoroid condition, but in opposite directions. In *Conta,* the trend has been for the crenulated surfaces of each side to diverge laterally so that the apparatus is broad as seen in dorsal view. In Sisorini, however, the crenulated surfaces approach the midline, and the apparatus is narrow. The primitive condition for the homologous structures in other members of Sisoridea is somewhere between the two derived conditions and cannot be unambiguously said to be more similar to either of them.

The parallel occurrence of such similar stridulatory mechanisms within Sisoridea is intriguing, especially considering that the complex is unknown elsewhere in siluriforms. Nonetheless, there are synapomorphic modifications of sisoroids that can be interpreted as precursors to the stridulatory mechanism seen in some members of the group. As described for character 91, the ventral portion of the first nuchal plate and the distal tip of the neural spine of the complex centrum contact one another by a modified surface in all members of Sisoridea. These modified surfaces are positionally homologous to the sound-producing ridged surfaces of the stridulatory apparatus. Moreover, in several cases the contacting surfaces have a rough texture, indicating that whatever their function may be in the plesiomorphic sisoroid state, friction is important, just as with the ridged surfaces of the stridulatory apparatus. The transformation from the typical sisoroid condition to that of a fully formed stridulatory apparatus is therefore not difficult to visualize. The stridulatory complex is certainly more similar to the situation in generalized sisoroids than to the primitive siluriform condition.

The functional significance of the sisoroid modifications of the supraneural and neural spine of the complex centrum (character 91) are unknown. These structures may also be involved in a sound-producing mechanism, although obviously a less efficient one than that of the Sisorini and *Nangra.* It is equally possible that these modifications serve as a reinforced mechanical tie between the dorsal fin complex and the vertebral column. Whatever the case may be, it is plausible that the repeated occurrence of such an unusual structure as the stridulatory apparatus in some sisoroids is in part accounted for by the preadaptation represented by specializations in the supraneural and corresponding neural spine typical of all the Sisoroidea.

The case of the nonhomology of the stridulatory apparatus is an example of the importance of completeness of taxonomic representation in phylogenetic studies. The hypothesis of nonhomology is dependent on the presence of taxa without the mechanism phylogenetically located between *Conta* and Sisorini in the cladogram. It is only through the inclusion of those taxa in the analysis that optimization procedures bearing on a hypothesis of nonhomology become conclusive. In the absence of taxa such as the aspredinids, *Bagarius,* and Glyptosterninae in this analysis, the nonhomology of the sound-producing mechanism could not possibly be discovered, no matter how accurate the hypothesis might otherwise be. Reasons for not including certain taxa can range from unavailability for study to extinction prior to discovery. Whichever the reason, it is clear that the completeness of taxonomic representation is critical for hypotheses of character evolution, a conclusion that was corroborated in a previous study dealing with a different group of fishes (Stiassny & de Pinna, 1994) and in others dealing with fossil taxa (Gauthier et al., 1988; Donoghue et al., 1989).

Evolution of the Thoracic Adhesive Apparatus

The hypothesis of phylogenetic relationships among sisoroids presented here permits a more objective insight into the evolution of adhesive modifications in the group. This topic, in connection with the broader question of adaptations to torrential environments, has been the object of copious discussion in the past, and much difference of opinion has been the result of exiguous knowledge about relationships among the various taxa involved. As described in the discussion of character 110, the thoracic adhesive apparatus is formed by a series of roughly parallel integumentary ridges and grooves, the ridges having a dense covering of unculi. This structure, in a thoracic and/or abdominal location, is unique within Siluriformes.

The optimization of the character in the most-parsimonious hypothesis makes it clear that the thoracic adhesive apparatus, as defined here, originated twice within sisoroids: once in Glyptosterninae and again in Erethistidae. In both cases, the character is subsequently reversed in a subgroup. Within Glyptosterninae, the adhesive apparatus is hypothesized as secondarily lost in the subtribe Glyptosternina ("glyptosternoids"), and within erethistids a similar reversal happens in the tribe Erethistini. In both cases, an alternative optimization of the character is possible, in which the adhesive apparatus is independently developed in Continae and Laguviini (of Erethistidae) and in Glyptothoracini and Pseudecheneidina (of Glyptosterninae). However, for reasons presented elsewhere (de Pinna, 1991), optimizations maximizing reversals (ACCTRAN) are theoretically preferable and therefore adopted as the favored alternative of character evolution. In accordance with this reasoning, the adhesive apparatus is considered homologous in Continae and Laguviini and in Glyptothoracini and Pseudecheneidina.

A hypothesis of nonhomology of the apparatus in Glyptosterninae and Erethistidae is not subject to considerations regarding treatment of ambiguous optimizations. The transitions are unambiguously convergent, and it is impossible to consider these two occurrences of the thoracic apparatus as homologous without violating parsimony. As with the stridulatory apparatus, it is puzzling that such a distinctive and unique structure within siluriforms has arisen twice in a relatively small group distributed in the same general area. One explanation that is always possible when tracing character evolution is that there are unknown taxa (extinct or not yet discovered) with the apparatus that would fit into key positions in the cladogram and overturn the optimization. For example, two successive sister groups to Sisorinae that happened to have the apparatus would suffice to reconfigure the optimization in such a way that the structure would then be hypothesized as homologous in all taxa. Thus, the inferred convergence may be an artifact of incomplete taxonomic representation. This scenario, although always a possibility, cannot affect the current hypothesis unless the relevant taxa are actually found.

If we accept the hypothesis that the thoracic apparatus actually originated twice within sisoroids, we can look for some character in sisoroids in general that may have served as a preadaptation for the development of the structure. Roberts (1982) reported that *Bagarius,* a fish lacking the adhesive apparatus as defined here and in other papers, has well-defined patches of unculi over some areas of the skin. Such well-circumscribed patches differ from the more diffuse condition common in other ostariophysans and resemble those present, for example, at the edges of the apparatus in *Conta* (Figs. 50A,B). If the presence of these patches is confirmed in additional sisoroid taxa, it is possible that what is here called the adhesive apparatus is in fact an extreme condition of a widespread modification found in other sisoroids. If so, then the explanation for the repeated occurrence of the adhesive apparatus in closely related taxa is the same offered above for a similar situation observed for the stridulatory mechanism, i.e., the presence of a synapomorphic condition for a more inclusive group that served as a precursor.

Another intriguing aspect of the evolution of the adhesive apparatus as inferred from the proposed phylogeny is its reversal in Glyptosternina and Erethistini. There is little doubt that the adhesive apparatus is important in providing the fish with a means of maintaining its position against strong currents, i.e., as an organ of attachment to the substrate. One would expect, therefore, that the taxa that lost the adhesive apparatus would be those that secondarily occupied lentic environments. This is not always the case, however. The Glyptosternina comprises some of the fishes most highly adapted for torrential life, and all of them lack the thoracic apparatus (although they have other morphological specializations for that environment). Among members of Erethistini, *Hara* and *Erethistes* are reported to inhabit muddy sluggish waters overgrown with vegetation (Hora, 1950, pp. 189–190; Jayaram, 1973, p. 388), but there is some discrepant information about *Erethistoides* (the sister group to the remainder of the tribe, lacking the thoracic apparatus). According to Hora (1950, pp. 190, 192) the genus is known to occupy fast-running waters, but Jayaram (1973, p. 388) stated that "*Erethistes montana* [= *Erethistoides montana*] and *Hara hara* were collected from shallow sluggish rivers of the Teesta drainage system." Clearly, more detailed information on the biology of erethistids and sisorids is needed for a more conclusive discussion of the adaptive/phylogenetic significance of the thoracic adhesive apparatus.

A number of parallel adaptations to torrential environments have been previously observed between Sisoridae and the Neotropical Loricariidae and Astroblepidae (cf. Hora, 1930). However, the most striking example of adaptation to life in tor-

rents among Neotropical catfishes is found in the family Trichomycteridae. The organs of attachment in that family are represented by modified opercular and interopercular bones armed with enlarged odontodes at their margins, a set of modifications that is synapomorphic for the family. Contrary to the situation in other catfishes with organs of attachment, some trichomycterids have modified these adaptations for parasitic habits rather than for resisting water currents. In such cases, the attachment organs are used to penetrate and fix the parasitic fish inside its feeding site on the host (Gudger, 1930; Kelley & Atz, 1964; Machado & Sazima, 1983). Nevertheless, most trichomycterids, including the basal subfamilies Copionodontinae and Trichogeninae (successive sister groups to the remainder of the family; de Pinna, 1992), indeed use the attachment organs for life in torrents, indicating that this is the primitive functional role of the mechanism in the family. In trichomycterids that are neither parasitic nor inhabitants of torrential waters, there tends to be reduction or loss of the opercular and interopercular armature for attachment. Such is the case with several sand-dwelling members of the subfamilies Glanapteryginae and Sarcoglanidinae (Myers, 1944; Myers & Weitzman, 1966; de Pinna, 1989). Most trichomycterids inhabit fast-running waters, often small creeks, and occur in nearly all highlands and mountainous regions in South America on both sides of the Andes. The torrent-inhabiting trichomycterids use their "adhesive" mechanism not only to resist currents but also to actively move against them and climb waterfalls. Their "elbowing" head movement to ascend currents has been described on some occasions (e.g., Eigenmann, 1918, p. 262). Upriver migratory activities have been described for *Trichomycterus migrans* (cf. Dahl, 1960).

Because of their comparable levels of diversification and their adaptations to similar environments, a comparison between the patterns of diversity displayed by trichomycterids and sisoroids reveals some common elements about the evolutionary significance of adhesive adaptations. Within sisoroids, the most speciose clade is Glyptosterninae, with close to 50% of all species in the superfamily. This clade is apomorphically diagnosed by the thoracic adhesive apparatus. Their sister group, subfamily Sisorinae, lacks such adaptations, and includes only about 15 species. In trichomycterids, the situation is more complex because very few members of the family lack the attaching mechanism. But all clades that are apo-

morphically diagnosed by the lack of the opercular and interopercular armature are small in absolute number of species. Nematogenyiidae, the sister group to Trichomycteridae (de Pinna, 1992), lacks the opercular and interopercular armature and includes a single species (*Nematogenys inermis*) endemic to a small area in central Chile. Thus, in both trichomycterids and sisorids, the presence of attaching mechanisms seems to have been a determining factor for their distribution over wide areas and their concomitant diversification.

One can say that the Andes are for trichomycterids what the Himalayas are for sisorids and erethistids. Both mountain chains represent a vast environment where adhesive and anchoring adaptations are obviously an advantage for dispersal over wide areas. Such wide distribution is prone to high levels of vicariant events. As expected, sisorids and trichomycterids are the most diverse and widely distributed siluriforms groups around each of those mountain chains.

Relationships of the Neotropical Aspredinidae

The family Aspredinidae is the most aberrant component of the Neotropical catfish fauna. The family's relationships have always been obscure, and there have been few explicit proposals about its possible closest relatives. Even the internal anatomy of aspredinids has rarely been studied, a situation that by and large continues to the present. Chardon (1967) proposed that aspredinids were related to loricarioids, composed the Neotropical families Nematogenyidae, Trichomycteridae, Callichthyidae, Scoloplacidae, Loricariidae, and Astroblepidae. There is long-standing evidence that these six families form a natural group (e.g., Peyer, 1922), and more recent phylogenetic treatment has strongly supported the monophyly of loricarioids (Baskin, 1973; Schaefer & Lauder, 1986; Schaefer, 1990). Chardon's (1967) proposal was that aspredinids should be added to that assemblage. However, subsequent studies showed that Aspredinidae did not actually share any putative synapomorphies exclusively with loricarioids (Baskin, 1973). That family has remained incertae sedis within Siluriformes until recently, probably more as a result of the paucity of studies than because of real controversy.

The anatomical distinctiveness of aspredinids puts a large gap between it and other Neotropical

catfish families. Comparisons restricted in their coverage to a single continent will meet with difficulty finding any special similarities joining aspredinids with any other Neotropical family or group of families. The first suggestion that aspredinids might be related to non-Neotropical taxa was by Ferraris (1989), who proposed that they were the sister group to the Akysidae. Although Ferraris's results were not published in full, they stimulated renewed interest in the problem and for the first time raised the possibility that the relationships of aspredinids might be outside the Neotropics.

The hypothesis presented in this study for the placement of Aspredinidae relies on evidence at several levels. The evidence for individual clades is not particularly overwhelming, but the total evidence for all internested clades bearing on aspredinid relationships is rather strong. Aspredinids share with the other members of Sisoroidea seven synapomorphies (nos. 1, 32, 61, 64, 77, 87, 91). Of these, four (nos. 32, 61, 64, 91) are unreversed and nearly unique within siluriforms. The presence of the humerovertebral ligament (character 64), in particular, has not so far been observed in any other catfishes. The group called clade A above (Akysidae + Sisoridae + Erethistidae + Aspredinidae) relies on three synapomorphies; one of these (no. 24) shows reversals, and the other two (nos. 26, 90) have a number of putatively homoplastic occurrences elsewhere in siluriforms. Support for this clade is therefore weak. Another group including aspredinids, clade B (Aspredinidae + Sisoridae + Erethistidae), is supported by 10 characters (nos. 27, 57, 62, 64, 66, 77, 79, 87, 88, 103), two of which (nos. 77, 87) are reversals. Although several of the other characters are themselves reversed within the clade, most of the reversals are concentrated in the highly modified tribe Glyptosternini, in particular in the subtribe Glyptosternina. The sister-group relationship between aspredinids and erethistids (clade C) relies on five characters (nos. 3, 38, 84, 85, 97), of which only one (no. 97) is neither reversed nor convergent elsewhere in sisoroids.

The placement of aspredinids within an internested set of sisoroids, therefore, is supported by a total of 25 character transitions at several levels. Of these clades, the strongest seems to be the one joining sisorids, aspredinids, and erethistids (clade B). This clade is supported by the largest set of synapomorphies, and five extra steps are needed to collapse it. This is more steps than it takes to collapse any other component involving aspredi-

nids, except for the whole superfamily. In comparison, clade C and clade A both collapse at a single extra step. Therefore, although the relationships of aspredinids with erethistids alone are relatively fragile, their relationships with erethistids and sisorids are robust. Thus, in terms of the biogeographical significance of hypothesized relationships, the alignment of Neotropical aspredinids with Asiatic taxa can be considered well corroborated.

A remarkable process of skin molting so far observed only in aspredinids and akysids may eventually help define some sisoroid subgroups. Ferraris (1991, pp. 86, 87, 164) reported that aspredinids and the akysid *Breitensteinia* have been observed in aquarium conditions to shed their skin periodically. According to Ferraris, in *Breitensteinia* the newly exposed skin is brighter than the old layer and shows the pigmentation pattern very vividly. Also, the skin is shed in large straps, occasionally in a nearly entire piece that looks like a peel of the fish. Both aspredinids and akysids have a very similar skin surface, with a rough texture and numerous large tubercles. The nature of their probably heavily keratinized skin may necessitate periodic molting. If this is so, skin shedding should also be searched for in sisorids and erethistids, most of which have a similar skin texture, though normally less extreme. Unfortunately, skin molting has to date been observed only accidentally and has never been studied in any detail; Ferraris's (1991) report seems to be the first and only published reference to the phenomenon. Sisoroids are only rarely kept in artificial conditions, and in the few cases observed the shed skin seems to be quickly consumed by other fish (Ferraris, 1991, p. 86), making it even less likely to be detected. Skin molting has so far not been observed in any other siluriforms, and it is certainly a process of considerable biological and systematic significance. More observations are critically needed to understand the phenomenon in a phylogenetic context.

The inclusion of aspredinids within sisoroids, a group otherwise distributed exclusively in Asia, seems to clearly represent a trans-Pacific relationship. This kind of relationship has been observed in numerous zoological and botanical taxa, and its biogeographical implications are important (cf. Croizat, 1958; Melville, 1981; Nelson & Platnick, 1981). A number of models have been proposed to explain trans-Pacific relationships, the most famous of which is the Pacifica hypothesis. That model postulates a former continent located around

the upcoming Pacific basin that split up into fragments, which then collided and fused with the continents presently around the Pacific rim (Hallier, 1912; Melville, 1966, 1967; Nur & Ben-Avraham, 1981). The Pacific Ocean, thus, originated between the rifting margins of Pacifica, and the expansion of the basin coincided with the fragmentation of the continent. The Pacifica hypothesis is controversial, but trans-Pacific relationships unquestionably provide support for it. Most cases of trans-Pacific relationships, however, relate North America and East/Southeast Asia and involve mainly plant taxa. Trans-Pacific relationships linking animal groups in South America and Asia are rare.

The nature of the trans-Pacific aspredinid/sisoroid relationship, however, is unclear. For it to be fully conclusive, sisoroids would have to contain some elements in Africa, and aspredinids would then have to be demonstrably closer to the Asiatic than to the African components. Only in that case would all elements relevant to the problem be present. Based on our current understanding of sisoroid distribution, the trans-Pacific hypothesis relies partly on the absence of known representatives of the group in Africa rather than on the known presence of taxa in all the relevant areas. Despite this, the relationships of aspredinids with Asiatic taxa is an intriguing phenomenon that deserves further study, perhaps using a data set of a different nature, and should stimulate the search for yet undiscovered fossil or recent sisoroids in Africa.

Acknowledgments

Literature Cited

ALEXANDER, R. M. 1965. Structure and function in the catfish. Journal of Zoology, 148: 88–152.

ARRATIA, G. 1987. Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): Morphology, taxonomy and phylogenetic implications. Bonner Zoologische Monographien, 24: 1–123.

———. 1992. Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. Bonner Zoologische Monographien, 32: 1–149.

ARRATIA, G., AND L. HUAQUIN. 1995. Morphology of the lateral line system and of the skin of diplomystid and certain primitive loricarioid catfishes and systematic and ecological considerations. Bonner Zoologische Monographien, 36: 1–110.

ARRATIA, G., AND H.-P. SCHULTZE. 1990. The urohyal: Development and homology within osteichthyans. Journal of Morphology, 203: 247–282.

BAILEY, R. M., AND J. N. BASKIN. 1976. *Scoloplax dicra*, a new armored catfish from the Bolivian Amazon. Occasional Papers of the Museum of Zoology, University of Michigan, **674**: 1–14.

BASKIN, J. N. 1973. Structure and relationships of the Trichomycteridae. Ph.D. diss., City University of New York, New York.

BEGLE, D. P. 1991. Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis. Systematic Zoology, **40**: 33–53.

BERG, L. S. 1940. Classification of fishes, both Recent and fossil. Travaux de l'Institut Zoologique de l'Academie des Sciences de l'URSS, **5**(2): 87–517.

BHATIA, B. 1950. Adaptive modifications in a hillstream catfish, *Glyptothorax telchitta* (Hamilton). Proceedings of the National Institute of Sciences of India, **16**(4): 271–285.

BLEEKER, M. P. 1853. Nalezingen op de ichthyologische fauna van Bengalen en Hindostan. Verhandelingen van het bataviaasch Genootschap van Kunsten en Wetenschappen, **25**: 1–164.

———. 1858. De visschen van den Indischen Archipel. Siluri. Acta Societatis Scientiarum Indo-Neerlandicae, **4**: 1–370 + xii.

———. 1862. Atlas Ichthyologique des Indes Orientales Néêrlandaises, publié sous les auspices du Gouvernement colonial néêrlandais. Tome II. Siluroïdes, Characoïdes et Hétérobranchoïdes. Government publication, Amsterdam.

———. 1863. Sistema silurorum revisum. Nederlandsch Tijdschrift voor de Dierkunde, **1**: 77–122.

———. 1873. Memoire sur la faune ichthyologique de Chine. Nederlandsch Tijdschrift voor de Dierkunde, **4**: 113–154.

BLYTH, E. 1858. Report of the Curator, Zoological Department, for May, 1858. Journal of the Asiatic Society of Bengal, **27**: 267–290.

———. 1860. Report on some fishes received chiefly from the Sitang River and its tributary streams, Tenasserim Provinces. Journal of the Asiatic Society of Bengal, **29**: 138–174.

BOESEMAN, M. 1966. A new sisorid catfish from Java, *Sundagagata robusta* gen. et spec. nov. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C Zoology, **69**: 242–247.

BOULENGER, G. A. 1904. Teleostei (systematic part), pp. 541–727. *In* Harmer, S. F., and A. E. Shipley, eds., The Cambridge Natural History, vol. 7. Macmillan, London.

BREMER, K. 1994. Branch support and tree stability. Cladistics, **10**: 295–304.

BRIDGE, T. W., AND A. C. HADDON. 1893. Contributions to the anatomy of fishes. II. The air-bladder and Weberian ossicles in the siluroid fishes. Philosophical Transactions of the Royal Society of London Series B, **84**: 65–333.

BROOKS, D. R., R. T. O'GRADY, AND E. O. WILEY. 1986. A measure of the information content of phylogenetic trees, and its use as an optimality criterion. Systematic Zoology, **35**: 571–581.

BROWN, B. A., AND C. J. FERRARIS. 1988. Comparative osteology of the Asian catfish family Chacidae, with the description of a new species from Burma. American Museum Novitates, **2907**: 1–16.

BURGESS, W. E. 1989. An Atlas of Freshwater and Marine Catfishes: A Preliminary Survey of the Siluriformes. TFH Publications, Neptune City, N.J.

CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics, **4**: 291–296.

CHARDON, M. 1967. Reconnaissance d'un groupe naturel de six familles de Siluriformes Sud-Américains grâce à l'étude anatomique de l'appareil de Weber au sens large. Annales de la Societe Royale Zoologique de Belgique, **97**(1): 35–38.

———. 1968. Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. Annales du Musee Royale de l'Afrique Centrale Serie 8, **169**: 1–277.

CHAUDHURI, B. L. 1919. Report on a small collection of fish from Putao (Hkamti Long) on the northern frontier of Burma. Records of the Indian Museum, **16**: 271–287, pl. 22.

CHEN, X. 1994. Phylogenetic studies of the amblycipitid catfishes (Teleostei, Siluriformes) with species accounts. Ph.D. diss., Duke University, Durham. [Not seen.]

CHEN, X., AND J. G. LUNDBERG. 1995. *Xiurenbagrus*, a new genus of amblycipitid catfishes (Teleostei: Siluriformes), and phylogenetic relationships among the genera of Amblycipitidae. Copeia, **1995**(4): 780–800.

CHU, X.-L. 1979. Systematics and evolutionary pedigree of the glyptosternoid fishes (family Sisoridae). Acta Zootaxonomica Sinica, **4**(1): 72–82. [In Chinese.]

———. 1981. Taxonomic revision of the genera *Pareuchiloglanis* and *Euchiloglanis*. Zoological Research, **2**(1): 25–31. [In Chinese.]

———. 1982. Phylogeny of the genus *Pseudecheneis* (Siluriformes, Sisoridae), with descriptions of two new species. Acta Zootaxonomica Sinica, **7**(4): 428–437. [In Chinese.]

COAD, B. W. 1981. *Glyptothorax silviae*, a new species of sisorid catfish from southwestern Iran. Japanese Journal of Ichthyology, **27**(4): 291–295.

COAD, B. W., AND G. B. DELMASTRO. 1985. Notes on a sisorid catfish from the Black Sea drainage of Turkey. Cybium, **9**(3): 221–224.

CROIZAT, L. 1958. Panbiogeography. Published by the author, Caracas, Venezuela.

DAHL, G. 1960. Nematognathous fishes collected during the Macarena Expedition, 1959. Novedades Colombianas, **1**(5): 302–317.

DAY, F. 1871. On the freshwater siluroids of India and Burmah. Proceedings of the Zoological Society, London, **1871**: 703.

———. 1873. Report on the Fresh Water Fish and Fisheries of India and Burma. Office of the Superintendent of Government Printing, Calcutta, India.

DING, R.-H., T.-Y. FU, AND M.-R. YE. 1991. Two new species of the genus *Pareuchiloglanis* from China. Acta Zootaxonomica Sinica, **6**(3): 369–374. [In Chinese.]

DINGERKUS, G., AND C. UHLER. 1977. Enzyme clearing of alcian-blue stained whole small vertebrates for demonstration of cartilage. Stain Technology, **52**: 229–232.

DONOGHUE, M., J. DOYLE, J. GAUTHIER, A. KLUGE, AND T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. Annual Review of Ecology and Systematics, **20**: 431–460.

DURAND, J. 1949. Les formes jeunes du *Pangasianodon gigas* Chevey. Le genre *Pangasianodon.* Buletin de la Société Zoologique de France, **74**: 112–116.

EIGENMANN, C. H. 1918. The Pygidiidae, a family of South American catfishes. Memoirs of the Carnegie Museum, **7**: 259–398.

ELDREDGE, N., AND J. CRACRAFT. 1980. Phylogenetic Patterns and the Evolutionary Process. Columbia University Press, New York.

ESCHMEYER, W. N. 1990. Catalog of the Genera of Recent Fishes. California Academy of Sciences, San Francisco.

FARRIS, J. S. 1969. A successive approximations approach to character weighting. Systematic Zoology, **18**: 374–385.

———. 1983. The logical basis of phylogenetic analysis, pp. 7–36. *In* Platnick, N. I., and V. A. Funk, eds., Advances in Cladistics, vol 2. Columbia University Press, New York.

———. 1988. Hennig86, version 1.5. Distributed by the author, Port Jefferson Station, N.Y.

FERRARIS, C. 1988. The Auchenipteridae: Putative monophyly and systematics, with a classification of the Neotropical doradoid catfishes (Ostariophysi, Siluriformes). Ph.D. diss., City University of New York, New York.

———. 1989. On the interrelationships between the Aspredinidae and the Akysidae (Ostariophysi, Siluriformes), p. 86. *In* Abstracts of the 69th Annual Meeting, American Society of Ichthyologists and Herpetologists. ASIH, Arizona State University, Tempe.

———. 1991. Catfish in the Aquarium. Tetra Press, Morris Plains, N.J.

FINK, S. V., AND W. FINK. 1981. Interrelationships of the ostariophysan fishes (Pisces, Teleostei). Zoological Journal of the Linnean Society, **72**: 297–353.

FITZHUGH, K. 1989. Cladistics in the fast lane. Journal of the New York Entomological Society, **97**: 234–241.

FRIEL, J. P. 1994. A phylogenetic study of the Neotropical banjo catfishes (Teleostei: Siluriformes: Aspredinidae). Ph.D. diss., Duke University, Durham.

GAUBA, R. K. 1962. The endoskeleton of *Bagarius bagarius* (Ham.), part I—The skull. Agra University Journal of Research, **11**(1): 75–90.

———. 1966. Studies on the osteology of Indian sisorid catfishes—II. The skull of *Glyptothorax cavia.* Copeia, **1966**: 802–810.

———. 1967. Studies on the skull of the Indian Sisorid catfish, *Erethistes pussilus.* Journal of Zoology London, **151**: 379–388.

———. 1968. On the morphology of the skull of catfish *Pseudecheneis sulcatus.* Zoologische Anzeiger, **181**: 226–236.

———. 1969. The head skeleton of *Glyptosternum reticulatum* McClelland & Grifith. Monitore Zoologico Italiano, **3**: 1–17.

———. 1970a. Contributions on the skull of a catfish, *Erethistoides montana* Hora. Zoologische Beiträge, **15**: 185–201.

———. 1970b. On the cranial osteology of two Indian catfishes of the genus *Laguvia.* Zoologische Anzeiger, **185**: 55–67.

GAUTHIER, J., A. G. KLUGE, AND T. ROWE. 1988. Amniote phylogeny and the importance of fossils. Cladistics, **4**: 105–209.

GEOFFROY ST. HILLAIRE, I. 1829. Histoire Naturelle des Poissons du Nil, pp. 141–338. *In* Description de l'Egypte (ed. Commission des Monuments de l'Egypte), 2nd ed., vol. 24. C. L. F. Panckoucke, Paris.

GILL, T. 1861. Synopsis of the genera of the sub-family of Pimelodinae. Proceedings of the Boston Society of Natural History, **8**: 46–55.

———. 1872. Arrangement of the families of fishes, or classes Pisces, Marsipobranchii, and Leptocardii. Smithsonian Miscellaneous Collection, **247**: 1–49 + xlvi.

GOODRICH, E. S. 1909. Vertebrata craniata (first fascicle: cyclostomes and fishes), pp. xvi + 1–518. *In* Lankester, R., ed., A Treatise on Zoology, part 9. Adam and Charles Black, London.

GOULDING, M. 1980. The Fishes and the Forest: Explorations in Amazonian Natural History. University of California Press, Berkeley.

GRANDE, L. 1987. Redescription of †*Hypsidoris farsonensis* (Teleostei, Siluriformes), with a reassessment of its phylogenetic position. Journal of Vertebrate Paleontology, **7**: 24–54.

GRANDE, T. 1994. Phylogeny and paedomorphosis in an African family of freshwater fishes (Gonorynchiformes: Kneriidae). Fieldiana: Zoology, **78**: 1–20.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History, **131**: 341–455.

GUDGER, E. W. 1930. On the alleged penetration of the human urethra by an Amazonian catfish called candiru, with a review of the allied habits of other members of the family Pygidiidae, parts I and II. American Journal of Surgery, **8**: 170–188, 443–457.

GÜNTHER, A. 1864. Catalogue of the Fishes in the British Museum, vol. 5. British Museum of Natural History, London.

HADDON, A. C. 1881. On the stridulating apparatus of *Callomystax gagata.* Journal of Anatomy, **15**: 323–326.

HALLIER, H. 1912. Über frühere Landbrücken, Pflanzen- und Völkerwanderungen zwischen Australaien und Amerika. Mededeelingen van's Rijks Herbarium, **13**(13): 1–32.

HAMILTON, F. 1822. An Account of the Fishes Found in the River Ganges and Its Branches. Edinburgh.

HE, M., AND Y. CHEN. 1981. Two new catfishes of the genus *Akysis* from China. Zoological Research, **2**(3): 209–214. [In Chinese.]

HENNIG, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.

———. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.

———. 1968. Elementos de una Sistemática Filogenética. Editorial Universitaria de Buenos Aires, Rivadavia.

HERRE, A. W. 1940. New species of fishes from the Malay Peninsula and Borneo. Bulletin of the Raffles Museum, **16**: 5–26.

HORA, S. L. 1921. On some new or rare species of fish from the eastern Himalayas. Records of the Indian Museum, **22**: 731–744.

———. 1922. Structural modifications in the fish of mountain torrents. Records of the Indian Museum, **24**: 31–61.

———. 1923. Notes on fishes in the Indian Museum. V. On the composite genus *Glyptosternon* McClelland. Records of the Indian Museum, **25**: 1–44.

———. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. Philosophical Transactions of the Royal Society of London Series B, **218**: 171–282.

———. 1936. Siluroid fishes of India, Burma and Ceylon. II. Fishes of the genus *Akysis* Bleeker. Records of the Indian Museum, **38**: 199–202.

———. 1937. Notes on fishes in the Indian Museum— XXXVI. On a new genus of Chinese catfishes allied to *Pseudecheneis*. Records of the Indian Museum, **39**: 348–350.

———. 1950. Siluroid fishes of India, Burma and Ceylon. XIII. Fishes of the genera *Erethistes* Müller & Troschel, *Hara* Blyth and of two new allied genera. Records of the Indian Museum, **47**: 183–202.

———. 1952. Parallel evolution of *Pseudecheneis* Blyth and similar fishes of South-East Asia. Journal of the Asiatic Society, Science, **18**: 123–128.

HORA, S. L., AND P. CHABANAUD. 1930. The siluroid fish *Pseudecheneis* and an allied new genus. Records of the Indian Museum, **32**: 215–222.

HORA, S. L., AND N. C. LAW. 1941. Siluroid fishes of India, Burma and Ceylon. Records of the Indian Museum, **43**: 9–42.

HORA, S. L., AND A. S. MENON. 1948. Systematic position of three glyptosternoid fishes of the family Sisoridae (order Siluroidae). Proceedings of the National Institute of Sciences of India, **46**: 55–62.

HORA, S. L., AND E. G. SILAS. 1952a. Evolution and distribution of glyptosternoid fishes of the family Sisoridae (order Siluroidea). Proceedings of the National Institute of Sciences of India, **18**: 309–322.

———. 1952b. Notes on fishes in the Indian Museum. XLVII. Revision of the glyptosternoid fishes of the family Sisoridae, with description of new genera and species. Records of the Indian Museum, **49**: 5–30.

HOWES, G. J. 1983. The cranial muscles of loricarioid catfishes, their homologies and value as taxonomic characters (Teleostei, Siluriformes). Bulletin of the British Museum of Natural History, Zoology, **45**: 309–345.

ICZN. 1985. International Code of Zoological Nomenclature, 3rd ed. University of California Press, Berkeley.

JAYARAM, K. C. 1973. Siluroid fishes of India, Burma and Ceylon. 18. Systematic position of the genus *Laguvia* Hora and its relationships. Records of the Zoological Survey of India, **67**: 385–389.

———. 1981. The Freshwater Fishes of India, Pakistan, Bangladesh, Burma and Sri Lanka—A Handbook. Zoological Survey of India, Calcutta.

KELLEY, W. A., AND J. W. ATZ. 1964. A pygidiid catfish that can suck blood from goldfish. Copeia, **1964**: 702–704.

KIMURA, S. 1934. Descriptions of the fishes collected from the Yangtze-kiang, China, by late Dr. K. Kishinouye and his party in 1927–1929. Journal of the Shanghai Science Institute, Section 3, **1**: 11–247.

KOTTELAT, M. 1983. A new species of *Erethistes* Müller & Troschel from Thailand and Burma (Osteichthyes: Siluriformes: Sisoridae). Hydrobiologia, **107**: 71–74.

KOTTELAT, M., AND C. VIDTHAYANON. 1993. *Boraras micros* a new genus and species of minute freshwater fish from Thailand (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters, **4**: 161–176.

LAL, M. B., A. N. BHATNAGAR, AND J. P. UNIYAL. 1966. Adhesive modifications of a hillstream fish *Glyptothorax pectinopterus* (McClelland). Proceedings of the National Academy of Sciences India, **36**: 109–116.

LI, S. 1986. Systematics, distribution and evolution of *Glyptothorax* (Siluriformes: Sisoridae), pp. 521–528. *In* Uyeno, T., R. Arai, T. Taniuchi, and K. Matsuura, eds., Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan, Tokyo.

LUNDBERG, J. G. 1970. The evolutionary history of North American catfishes, family Ictaluridae. Ph.D. diss., University of Michigan, Ann Arbor.

———. 1975. Homologies of the upper shoulder girdle and temporal region bones in catfishes (order Siluriformes), with comments on the skull of the Helogenidae. Copeia, **1975**: 66–74.

———. 1982. The comparative anatomy of the toothless blindcat, *Trogloglanis pattersoni* Eigenmann, with a phylogenetic analysis of the ictalurid catfishes. Miscellaneous Publications of the Museum of Zoology, University of Michigan, **163**: 1–85.

LUNDBERG, J. G., AND J. N. BASKIN. 1969. The caudal skeleton of catfishes, order Siluriformes. American Museum Novitates, **2399**: 1–49.

MACHADO, F. A., AND I. SAZIMA. 1983. Comportamento alimentar do peixe hematófago *Branchioica bertonii* (Siluriformes, Trichomycteridae). Ciência e Cultura, **35**: 344–348.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology, **33**: 83–103.

MAGO-LECCIA, F. 1978. Los peces de la familia Sternopygidae de Venezuela. Acta Científica Venezolana, **29**: 1–89.

MAHAJAN, C. L. 1963. Sound producing apparatus in an Indian catfish *Sisor rhabdophorus* Hamilton. Journal of the Linnean Society, Zoology, **44**: 721–724.

———. 1966a. Sensory canals of the head in *Sisor rhabdophorus* Hamilton. Transactions of the American Microscopical Society, **85**: 548–555.

———. 1966b. *Sisor rhabdophorus*—A study in adaptation and natural relationship. I. The head skeleton. Journal of Zoology London, **149**: 365–393.

———. 1967a. *Sisor rhabdophorus*—A study in adaptation and natural relationship. II. The interrela-

tionship of the gas bladder, Weberian apparatus, and membranous labyrinth. Journal of Zoology London, **151**: 417–432.

——. 1967b. *Sisor rhabdophorus*—A study in adaptation and natural relationship. III. The vertebral column, median fins and their musculature. Journal of Zoology London, **152**: 297–318.

——. 1967c. The integument, exoskeleton and cutaneous sense organs of *Sisor rhabdophorus* Hamilton. Proceedings of the National Institute of Sciences of India B, **33**: 27–36.

McClelland, J. 1842. On the freshwater fishes collected by William Grifith, Esq., F. L. S. Madras Medical Service, during his travels under the orders of the Supreme Government of India, from 1835 to 1842. Journal of Natural History, Calcutta, **2**: 560–589.

Melville, R. 1966. Continental drift, mesozoic continents and the migrations of the angiosperms. Nature, **211**: 116–120.

——. 1967. The distribution of land around the Tethys Sea and its bearing on modern plant distribution, pp. 291–310. *In* Adams, C. G., and D. V. Ager, eds., Aspects of Tethyan Biogeography, no. 7. The Systematics Association, London.

——. 1981. Vicarious plant distributions and paleogeography of the Pacific region, pp. 238–274. *In* Nelson, G., and D. Rosen, eds., Vicariance Biogeography: A Critique. Columbia University Press, New York.

Menon, M. A. S. 1954. Notes on fishes of genus *Glyptothorax*. Records of the Indian Museum, **52**: 27–54.

Misra, K. S. 1976. The Fauna of India and the Adjacent Countries—Pisces, vol. III. Zoological Survey of India, Calcutta.

Mo, T. 1991. Anatomy, Relationships and Systematics of the Bagridae (Teleostei: Siluroidei)—With a Hypothesis of Siluroid Phylogeny. Theses Zoologicae 17. Koeltz Scientific Books, Königstein.

Mo, T., and X. Chu. 1986. A revision of the sisorid catfish genus *Glyptothorax* from China. Zoological Research, 7: 339–350. [In Chinese.]

Müller, J., and F. H. Troschel. 1849. Beschreibung und Abbildung neuer Fische; die Familie Characinen. Horae Zoologicae, 3: 1–27.

Myers, G. S. 1944. Two extraordinary new blind nematognath fishes from the rio Negro, representing a new subfamily of Pygidiidae, with a rearrangement of the genera of the family and illustrations of some previously described genera and species from Venezuela and Brazil. Proceedings of the California Academy of Sciences, 23: 591–602.

Myers, G. S., and S. H. Weitzman. 1966. Two remarkable new trichomycterid catfishes from the Amazon basin in Brazil and Colombia. Journal of Zoology, **149**: 277–287.

Nelson, G. J., and N. I. Platnick. 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia University Press, New York.

Nelson, J. S. 1994. Fishes of the World, 3rd ed. John Wiley & Sons, New York.

Nixon, K. C. 1992. CLADOS, version 1.0. Distributed by the author, Ithaca, New York.

Nixon, K. C., and J. I. Davis. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics, 7: 233–241.

Nur, A., and Z. Ben-Avraham. 1981. Lost Pacifica continent: a mobilistic speculation, pp. 341–358. *In* Nelson, G., and D. Rosen, eds., Vicariance Biogeography: A Critique. Columbia University Press, New York.

Peyer, B. 1922. Über die Flossenstacheln der Welse und Panzerwelse, sowie des Karpfens. Morphologisches Jahrbuch, **51**: 493–554.

de Pinna, M. C. C. 1989. A new sarcoglanidine catfish, phylogeny of its subfamily, and an appraisal of the phyletic status of the Trichomycterinae. American Museum Novitates, **2950**: 1–39.

——. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics, 7: 367–394.

——. 1992. A new subfamily of Trichomycteridae (Teleostei, Siluriformes), lower loricarioid relationships and a discussion on the impact of additional taxa for phylogenetic analysis. Journal of the Linnean Society, Zoology, **106**: 175–229.

——. 1993. Higher-level phylogeny of Siluriformes, with a new classification of the order (Teleostei, Ostariophysi). Ph.D. diss., City University of New York/American Museum of Natural History, New York.

de Pinna, M. C. C., and R. P. Vari. 1995. Monophyly and phylogenetic diagnosis of the family Cetopsidae, with synonymization of the Helogenidae (Teleostei: Siluriformes). Smithsonian Contributions to Zoology, **571**: 1–26.

Platnick, N. I., C. E. Griswold, and J. A. Coddington. 1991. On missing entries in cladistic analysis. Cladistics, **7**: 337–343.

Reed, H. D. 1924a. The morphology and growth of the spines of siluroid fishes. Journal of Morphology, **38**: 431–451.

——. 1924b. The morphology of the dermal glands in nematognathous fishes. Zeitschrift für Morphologie und Anthropologie, **24**: 227–264.

Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi. 2. Siluroidea. Annals and Magazine of Natural History, **8**: 553–577.

Reis, R. E. 1993. Filogenia da família Callichthyidae (Ostariophysi, Siluriformes), com uma revisão taxonômica do gênero *Hoplosternum*. Ph.D. diss., Tese de Doutoramento, Instituto de Biociências, Universidade de São Paulo, São Paulo.

Rieppel, O. 1988. Fundamentals of Comparative Biology. Birkhäuser Verlag, Basel.

Roberts, T. R. 1982. Unculi (horny projections arising from single cells), an adaptive feature of the epidermis of ostariophysan fishes. Zoologica Scripta, **11**: 55–76.

——. 1983. Revision of the south and southeast Asian sisorid catfish genus *Bagarius*, with description of a new species from the Mekong. Copeia, **1983**: 435–445.

——. 1989. The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia). Memoirs of the California Academy of Sciences, **14**: 1–210 + xii.

Roberts, T. R., and C. Vidthayanon. 1991. Systematic revision of the Asian catfish family Pangasiidae, with biological observations and descriptions of three new species. Proceedings of the Academy of Natural Sciences of Philadelphia, **143**: 97–144.

ROYERO, R. 1987. Morfologia de la aleta dorsal en los bagres (Teleostei: Siluriformes), con especial referencia a las familias americanas. Bachelor's thesis, Trabajo Especial de Grado, Universidad Central de Venezuela, Facultad de Ciencias, Caracas.

SAXENA, S. C., AND M. CHANDY. 1966. The pelvic girdle and fin in certain Indian hill stream fishes. Journal of Zoology London, 148: 167–190.

SCHAEFER, S. A. 1987. Osteology of Hypostomus plecostomus (Linnaeus), with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). Contributions in Science (Los Angeles), 394: 1–31 + iv.

———. 1990. Anatomy and relationships of scoloplacid catfishes. Proceedings of the Academy of Natural Sciences of Philadelphia, 142: 167–210.

SCHAEFER, S., AND G. V. LAUDER. 1986. Historical transformation of functional design: Evolutionary morphology of feeding mechanisms in loricarioid catfishes. Systematic Zoology, 35: 489–508.

SCHAEFER, S., S. H. WEITZMAN, AND H. A. BRITSKI. 1989. Review of the neotropical catfish genus Scoloplax (Pisces: Loricarioidea: Scoloplacidae) with comments on reductive characters in phylogenetic analysis. Proceedings of the Academy of Natural Sciences of Philadelphia, 141: 181–211.

SCHOCH, R. M. 1986. Phylogeny Reconstruction in Paleontology. Van Nostrand Reinhold, New York.

SCOPOLI, G. A. 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague.

SHELDEN, F. F. 1937. Osteology, myology, and probable evolution of the nematognath pelvic girdle. Annals of the New York Academy of Sciences, 37: 1–96.

SIEBERT, D. J. 1987. Interrelationships among families of the order Cypriniformes (Teleostei). Ph.D. diss., City University of New York, New York.

SINGH, N., AND N. K. AGARWAL. 1991. The SEM surface structure of the adhesive organ of Pseudocheneis sulcatus McClelland (Teleostei: Sisoridae), from Garhwal Himalayan hillstreams. Acta Ichthyologica et Piscatoria, 21(2): 29–35.

SKELTON, P. H. 1985. Two new Amphilius (Pisces, Siluroidei, Amphiliidae) from the Zaire River system, Africa. Revue de Zoologie Africaine, 99: 263–291.

SKELTON, P. H., L. RISCH, AND L. DE VOS. 1984. On the generic identity of the Gephyroglanis catfishes from southern Africa (Pisces, Siluroidei, Bagridae). Revue de Zoologie Africaine, 98: 337–372.

STEINITZ, H. 1961. Notes on some glyptosternoid fishes (Sisoridae, Siluroidea). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut, 59: 105–115.

STEYSKAL, G. C. 1980. The grammar of family-group names as exemplified by those of fishes. Proceedings of the Biological Society of Washington, 93: 168–177.

STIASSNY, M. L. J., AND M. C. C. DE PINNA. 1994. Basal taxa and the role of cladistic patterns in the evaluation of conservation priorities: A view from freshwater, pp. 235–249. In Forey, P. L., C. J. Humphries, and R. I. Vane-Wright, eds., Systematics and Conservation Evaluation. Systematics Association special volume 50. Clarendon Press, Oxford, England.

SWOFFORD, D. L. 1989. PAUP: Phylogenetic analysis using parsimony, version 3.0. Illinois Natural History Survey, Champaign.

SWOFFORD, D. L., AND W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. Mathematical Biosciences, 87: 199–229.

SWOFFORD, D. L., AND G. J. OLSEN. 1990. Phylogeny reconstruction, pp. 411–501. In Hillis, D. M., and C. Moritz, eds., Molecular Systematics. Sinauer, Sunderland, Mass.

TAVOLGA, W. N. 1962. Mechanisms of sound production in the ariid catfishes Galeichthys and Bagre. Bulletin of the American Museum of Natural History, 124: 1–30.

———. 1971. Sound production and detection, pp. 135–205. In Hoar, W. S., and D. J. Randall, eds., Fish Physiology, vol. 5. Academic Press, New York.

———. 1977. Sound Production in Fishes. Dowder, Hutchinson & Ross, Stroudsberg, Germany.

TAYLOR, W. R., AND G. VAN DYKE. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium, 9: 107–119.

TILAK, R. 1963. The osteocranium and the Weberian apparatus of the fishes of the family Sisoridae (Siluroidea): A study in adaptation and taxonomy. Zeitschrift für Wissenschaftliche Zoologie, 169: 281–320.

———. 1976. The adhesive thoracic apparatus in the evolution of glyptothoracoid fishes (Sisoridae: Siluriformes). Zoologische Anzeiger, 196: 255–261.

VARI, R. P. 1979. Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea). Bulletin of the British Museum of Natural History, Zoology, 36: 261–344.

WEBER, M., AND L. F. DE BEAUFORT. 1913. The Fishes of the Indo-Australian Archipelago. II. Malacopterygii, Myctophoidea, Ostariophysi: I. Siluroidea. Brill, Leiden.

WEITZMAN, S. H. 1954. The osteology and relationships of the South American characid fishes of the subfamily Gasteropelecinae. Stanford Ichthyological Bulletin, 4: 212–263.

———. 1962. The osteology of Brycon meeki, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin, 8: 1–77.

———. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. Bulletin of the American Museum of Natural History, 153: 327–478.

WEITZMAN, S. H., AND R. P. VARI. 1988. Miniaturization in South American freshwater fishes: An overview and discussion. Proceedings of the Biological Society of Washington, 101: 444–465.

WILEY, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. John Wiley & Sons, New York.

WILEY, E. O., D. SIEGEL-CAUSEY, D. R. BROOKS, AND V. A. FUNK. 1991. The compleat cladist: A primer of phylogenetic procedures. University of Kansas Museum of Natural History Special Publication, 19: 1–158 + x.

Yeates, D. 1992. Why remove autapomorphies? Cladistics, **8**: 387–389.

Zhou, W., & X.-L. Chu. 1992. A new species of *Pseu-decheneis* with comments on osteological differentiations at species level. Acta Zootaxonomica Sinica, **17**: 110–115.